

THE METABOLISM OF NICOTINIC ACID IN THE GREEN PEA AND ITS CONNECTION WITH TRIGONELLINE

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CONTENTS

§ 1.	The problem of the biosynthesis of nicotinic acid	123
2.	The determination of nicotinic acid and trigonelline	128
3.	The plant material	130
4.	The metabolism of nicotinic acid during the development of the pea	131
5.	The influence of external circumstances on the metabolism of nicotinic acid	133
6.	The transformation of nicotinic acid into trigonelline	135
7.	The effect of several compounds on the production of nicotinic acid	138
8.	Summary	141
	Literature	142

§ 1. THE PROBLEM OF THE BIOSYNTHESIS OF NICOTINIC ACID

In plants two groups of pyridine compounds are found. To the first group belongs the vitamin B₆ complex i.e. pyridoxine, pyridoxal and pyridoxamine. The function of these substances has as yet not been established. To the second group belong the nicotinic acid derivatives and the phosphopyridine nucleotides. These phosphopyridine nucleotides, which consist of two bases, the amide of nicotinic acid and adenine, two molecules ribose and phosphoric acid, are indispensable ingredients in the metabolism of every cell, because they act as hydrogen carrying coenzymes in respiratory processes. Therefore, the nicotinic acid (abbreviated as *niacin*), is found in all the plants, hitherto examined.

The pathway of the biosynthesis of the pyridine nucleus is not yet established. As we obtained no indications that the plant is able to transform pyridoxine into niacin, we restricted our investigations to the problem of the biosynthesis of niacin in plants.

The niacin cannot, however, be produced by all the organisms themselves. Those which have lost the capacity of synthesizing niacin, may be called *niacin-heterotrophic*. Such organisms, therefore, have to obtain niacin as an indispensable nutrient, a vitamin or a growth-factor. It is evident that by investigating the metabolism of niacin-

heterotrophic organisms, no further information can be obtained about the pathway in which the pyridine nucleus is formed naturally.

A large number of organisms, mammals as well as bacteria and the green plants are able to synthesize niacin from simpler compounds. These *niacin-autotrophic organisms* can only be used to investigate the biosynthesis of niacin. Broadly outlined two different methods of research have been followed.

The first method is based on a *comparative physiological examination* of organisms, in which the pathway of the biosynthesis of niacin is somewhere blocked. Then a number of feeding experiments are performed to investigate which compounds can replace niacin as a factor of growth.

Such investigations were performed with the aid of *Neurospora* mutants. In this case it was shown that *Neurospora crassa* mutant 65001, which needed niacin for growth, could also be grown when the medium contained indol, tryptophan, kynurenine or 3-hydroxy-anthranilic acid (BEADLE e.a. 1947; MITCHELL and NYC 1948). From this it was concluded that these compounds could be precursors in the biosynthesis of niacin (fig. 1).

In the second method of research an attempt was made to *influence directly the pathway* of the niacin metabolism in complete niacin-autotrophic organisms by adding supposed precursors to the organism. To perform this, the investigator has to determine quantitatively the amounts of substances concerned with the reactions.

Several mammals are able to produce large amounts of niacin when tryptophan is added to the food. These organisms, thereby, stabilize the niacin content in their tissues to a certain level by an increased excretion of niacin derivatives, especially N-methyl niacinamide (ROSEN e.a. 1946; SINGAL e.a. 1946; SARETT e.a. 1947; SCHWEIGERT 1947). The conclusion is often published that mammals transform tryptophan partly into niacin. However, tryptophan as well as niacin are intensively concerned in the metabolism of amino acids (KREHL 1949). This makes the interpretation of such experiments rather difficult. Furthermore, it was shown that the addition of ornithine to a suspension of *Escherichia coli* had a favourable effect on the niacin production, whereas this was not the case when tryptophan was added (ELLINGER and ABDEL KADER 1948-49).

Furthermore researches were made by means of *isotopic compounds*. The essence of the isotope technique in biochemical research consists in the preparation of a compound in which one or more of the atomic components have an abnormal isotope concentration. Thereupon "labeled" compounds are administered to the organism, and it is tested in which metabolic products the labeled atoms will be found back.

The question under discussion was traced by HEIDELBERGER e.a. (1948-49) with the use of labeled tryptophan. They gave several animals labeled tryptophan and tested the urine for labelled compounds. A young mature rabbit was injected subcutaneously with dl-tryptophan- β -C¹⁴ in isotonic saline and kynurenine was isolated from the urine with the radioactive C-atom in the β position. Further-

more young dogs were given dl-tryptophan- β -C¹⁴, and kynurenic acid was isolated from the urine. The labeled C-atom now was present in the 3-position of kynurenic acid. Through these investigations the breakdown of tryptophan to kynurenine and kynurenic acid, already known,

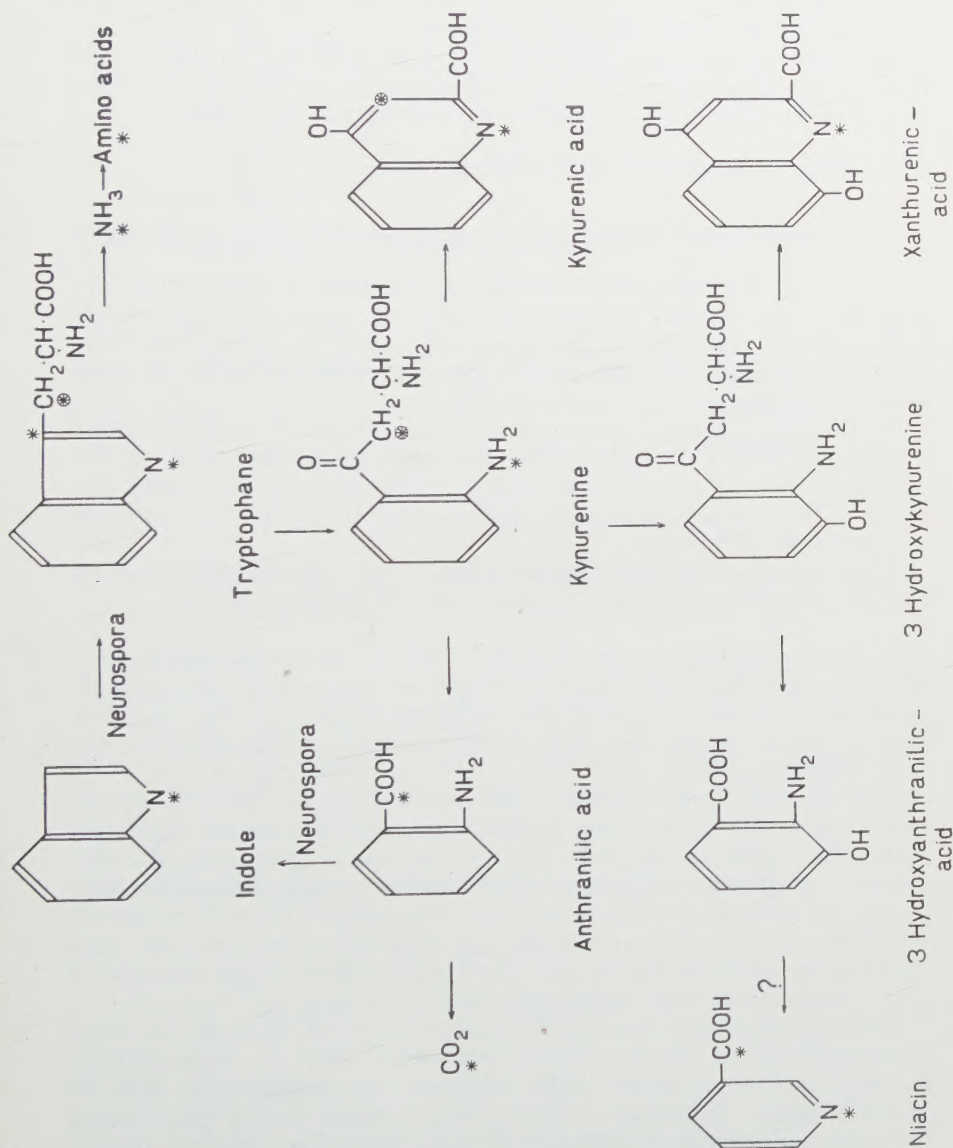


Fig. 1. Tryptophan and biochemically related compounds.

was ascertained. When finally dl-tryptophan- β -C¹⁴ was brought into the stomach of rats and the urine tested for N-methyl niacinamide, no radioactivity of this compound could be demonstrated. From the

above it results that in an eventual conversion of tryptophan into niacin the lateral chain of tryptophan must get lost. Later on 225 mg dl-tryptophan-3-C¹⁴ was given by stomach tube to rats after which 13.4 mg niacin with radioactive carboxylgroup was isolated from urine. In this way it is proved that this C-atom can be assimilated somehow in the carboxylgroup of niacin.

Then HEIDELBERGER e.a. point out that their results agree with those of the *Neurospora* investigations about the niacin synthesis from tryptophan. Therefore, the following conception was made:

tryptophan → kynurenine → kynurenic acid

↓

3-hydroxyanthranilic acid → niacin → N-methyl niacinamide

This kind of investigations, however, has some drawbacks. In the first place the labeled compounds prepared must, of course, be of such a nature that the isotopic atom will not be transferred by mere exchange. This for example may be the case with the carboxyl group and the aminogroup of amino acids.

Furthermore, there is an important breakdown of products added to the organism. This is also shown for indol, tryptophan and anthranilic acid (LEIFER e.a. 1950; SCHAYER 1950; NYC and MITCHELL e.a. 1949). The products of this breakdown may be assimilated again in the synthesis of niacin.

The conception of HEIDELBERGER e.a. is not the only explanation for the synthesis of niacin (BONNER and WASSERMAN 1950).

A few investigations are known in which the experiments were performed on *green plants*. Several investigators showed a strong niacin synthesis in germinating seeds and seedlings of the pea, the bean and cereals (BURKHOLDER e.a. 1942; TERROINE 1947-48; KLATZKIN 1948 and BANERJEE 1950).

The question may be asked whether the niacin synthesis in the green plant follows the same pathway as does the synthesis in mammals. The green plant does not excrete waste products like the animal does. An investigation into the precursors of niacin, therefore, is only possible in the following way. The plant is forced to absorb the compounds to be investigated, e.g. tryptophan or ornithine, and then the investigator has to analyse the plant whether an increase of niacin derivatives can be shown.

Such investigations were performed on leaves of cabbage, on those of broccoli and of tomato plants (GUSTAFSON 1949) on corn embryos in sterile culture (NASON 1949-1950) and on germinating seeds of *Phaseolus mungo* (BANERJEE 1950). Only a small rather insignificant increase of the niacin content after feeding tryptophan could be shown.

Contrary to the above mentioned investigations TERROINE e.a. (1948) could not show any increase of the niacin production in embryos of *Phaseolus vulgaris* in sterile culture when the culture solution contained tryptophan.

In this connection the earlier investigations may be mentioned of KLEIN and LINER (1932-33) in which a favourable effect of ornithine on the content of *trigonelline*, a methyl betaine of 3-pyridine carboxylic acid, was communicated. (fig. 2). They supposed, like ACKERMANN

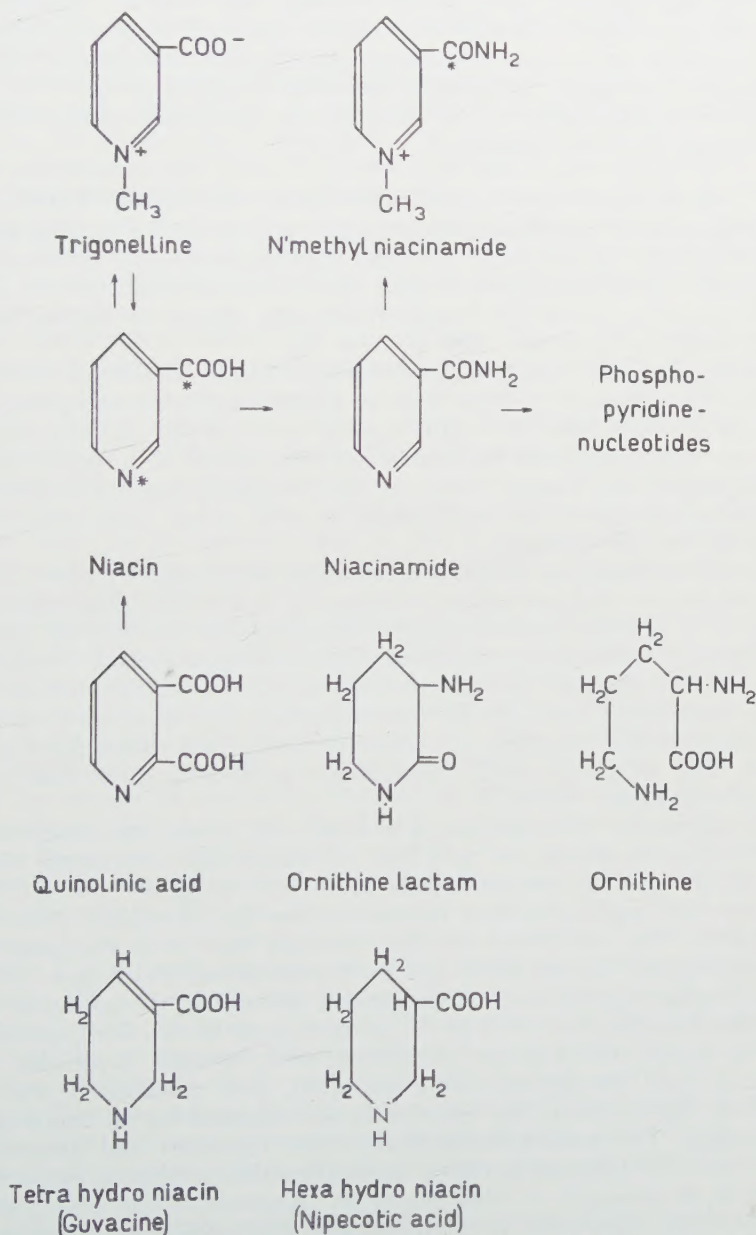


Fig. 2. Nicotinic acid (niacin) and biochemically related compounds.

(1913) had done, that trigonelline, which commonly occurs in plants, is formed niacin. Though even HENRY (1949) refers to these sources, the definite proof of this supposition has not yet been given.

The results of the investigations were in consequence contradictory as there are doubtful indications showing that besides tryptophan also ornithine may be involved in niacin synthesis by plants. Therefore, it will be important to examine which of the compounds above mentioned can effect the niacin synthesis in green plants.

Moreover, it is interesting to examine the conversion of niacin into trigonelline in green plants.

§ 2. THE DETERMINATION OF NICOTINIC ACID AND TRIGONELLINE

Nicotinic acid or *niacin* crystallizes in fine needles with a melting point of 229–232° C. It is soluble in water and ethanol, not, however, in ether. It is not destroyed by boiling with acids. All niacin derivatives which occur in plants are transformed into niacin by boiling with acids, except trigonelline and vitamin B₆.

Shortly after 1937 when the importance of niacin had become known, several investigators tried to find a quantitative determination. As early as 1943, a number of biological, spectrographic, colorimetric and microbiological determinations are mentioned in a survey made by ELVEHJEM and TEPLY. Only the microbiological and colorimetric determinations have been elaborated in such a way that they come in useful for our purpose.

A good *microbiological method* was found by SNELL and WRIGHT (1941) through the use of *Lactobacillus arabinosus* 17–5. For this microorganism niacin is a specific growth-factor; therefore, the growth of *Lactobacillus* in a medium, in which all other nutritious matter is present to excess, is a measure for the quantity of niacin. Niacin and niacinamide have equal activities for this organism. Cozymase and nicotinuric acid can also be used as a source of niacin, but trigonelline is inactive, like picolinic acid, isonicotinic acid and quinolinic acid (BARTON-WRIGHT 1944).

The *colorimetric determinations*, which are still in use, are based upon the reaction of König for pyridine, in which this compound reacts with CNBr and an aromatic amine, to give a yellow colour. This reaction has been used most extensively for the chemical estimation of niacin. The specificity of this reaction has been discussed by KRINGSTAD and NAESS (1939) and by WAISMAN and ELVEHJEM (1941). Amino acids, trigonelline, cozymase and vitamin B₆ do not cause this reaction. Pyridine and the 3-pyridine derivatives with a free 2-position, such as niacin, niacinamide, nicotinuric acid, nicotine, 3-picoline and nipecotic acid (hexahydro nicotinic acid), give a coloured reaction product. The course of the reaction is not identical for all compounds mentioned. The extinction-coefficient first increases and afterwards decreases. For different pyridine derivatives the maximum extinction, however, is obtained at other moments (KRINGSTAD and NAESS 1939, LAMB 1943). Therefore in plant extracts niacin derivatives must be transformed into niacin by hydrolysis. In the other way it is even

possible to determine niacin and niacinamide side by side in one solution (LAMB 1943; MELNICK and OSER 1943). The extinction of the reaction product in precisely fixed circumstances is directly proportional to the quantity of niacin. SWAMINATHAN (1938) established this for 10–50 micrograms in 25 ml. KRINGSTAD and NAESS (1939) indicate the proportion for 2–15 micrograms per ml. We did the same for 0.5–15 micrograms per ml.

Though the microbiological determination seems to be more specific and also allows a determination of smaller quantities of niacin, the complicated composition of the culture medium and the long incubation period of 72 hours is indeed a great drawback. The chemical determination proceeds along simpler and quicker lines. Disturbing compounds, however, have to be taken into consideration here. There is a great similarity between the niacin values obtained with the microbiological method and those obtained with the colorimetric method. So we used the latter method.

In combination with CNBr as aromatic amine we chose aniline, because a solution of this compound has no colour of its own and because it may be preserved for a long time if kept in the refrigerator.

The details concerning these niacin determinations have been published in our former publication (ZEIJLEMAKER 1951).

Trigonelline is a white crystalline compound, the melting point of which is 215–218° C. The hydrochloric addition product which is often used, has a melting point of 258° C. *Trigonelline* is soluble in water and ethanol. It is hydrolyzed with NaOH in high concentrations, but not with acids.

Trigonelline is found in 18 different families, belonging to divergent orders. So WEEVERS (1933–36) thought it was therefore very probable that *trigonelline* could be derived in a straightforward manner from a common product of metabolism. This might be niacin.

As is recorded in the literature upon the subject *trigonelline* should be found too in animals. ACKERMANN (1913) fed a dog with niacin and by means of mercuric chloride he obtained from the urine a precipitate which was considered to have been caused by *trigonelline*. As no blank test had been performed in which a dog was fed without niacin, it is not certain that the *trigonelline* found had been derived from the niacin. The greater part of the *trigonelline* found in urine appears to be derived from plant materials in the food (MELNICK et al. 1940). The animal organism probably does not produce any *trigonelline*, for ELLINGER and ABDEL KADER (1949) could not find *trigonelline* in the urine of several mammals when the food did not contain this compound. Meanwhile it was proved that practically all the methylated niacin previously determined and designated as *trigonelline* was indeed N-methyl niacinamide (HUFF and PERLZWEIG 1943). The processes of methylation which take place in the liver, apparently cannot include niacin, whereas they can include niacinamide (BACH 1945).

Different attempts were made to determine *trigonelline* quantitatively. A method as yet little used but very specific is the polaro-

graphic method. In this connection a number of pyridine derivatives have been examined by TOMPKINS and SCHMIDT (1942-43). It appeared that trigonelline could be determined polarographically with good results. Of the compounds which have been proved to occur in plants, only niacinamide can disturb the determination. However, this compound is converted into niacin by hydrolysis, after which process it no longer hinders. In conclusion we for our trigonelline determinations chose the polarographic method (ZEIJLEMAKER 1951).

The determinations of niacin and trigonelline in *plant material*, were always performed with series of 20 plants. The roots, the stems, the leaves and the cotyledons of each series of plants were cut off to work up similar parts together. Cutting the leaf-blades and the stipules of the leaves took so much time that in later investigations we worked up both stems and leaves of one series together. The plant material was ground in a mortar after the addition of 96 % ethanol, and transferred quantitatively into a beaker. The homogeneous mixture was weighed. A sample of it was extracted, hydrolyzed and prepared for the determinations (ZEIJLEMAKER 1951).

§ 3. THE PLANT MATERIAL

We used for our investigations *Pisum sativum* L. We chose a variety of the green pea with round yellow seeds, placed upon the market as "Ronde gele, Stam of Kruip" (height 40 cm). Among several varieties which could be investigated we were unable to establish any important differences of the niacin content (table I).

TABLE I

The niacin content in micrograms of a few varieties of *Pisum sativum* L.

Varieties examined	Per g material	Per pea	Weight of one pea
Stam of Kruip	12.4	2.9	0.232 g
Zelka	13.4	4.9	0.362 g
Unica	13.4	3.8	0.284 g
Mansholt	14.0	4.1	0.295 g
Stijfstroo CB	13.0	4.0	0.306 g
CB 3954	13.8	4.4	0.322 g

Before our experiments the seeds were selected according to the similarity of size and shape. We caused the peas to germinate between moist filterpaper in a room of constant temperature at 22° C. In summer the germinating percentage was about 100, only a few percents could not be nursed to full growth.

The seedlings of 4-5 days old were further bred on water cultures in the greenhouse. The culture solution was composed according to HOAGLAND and SHIVE (table II). About 10 plants were grown on each culture cylinder containing 2.5 liters of liquid. The solutions were aerated daily and renewed weekly (HOAGLAND 1937). In winter the cultures were given an extra illumination in the day time of 2

Neon high tension tubes and 2 white fluorescence tubes (Philips TL-tubes) at 75 cm distance.

The roots were not infected by *Bacterium radicola*.

Before starting the experiments plants of the same size were selected.

TABLE II

Composition of the culture solution for green plants according to HOAGLAND and SHIVE. To 1 liter of the solution A 1 ml of the solution B is added.

Solution A contains per l	Solution B contains per l
Ca(NO ₃) ₂ .4aq — 1.180 g	H ₃ BO ₃ — 2.86 g
MgSO ₄ .7aq — 0.493 g	MnCl ₂ .4aq — 1.81 g
KNO ₃ — 0.506 g	ZnSO ₄ .7aq — 0.22 g
KH ₂ PO ₄ — 0.136 g	Na ₂ MoO ₄ — 0.07 g
Fe-tartrate — 0.005 g	CuSO ₄ .5aq — 0.08 g

§ 4. THE METABOLISM OF NICOTINIC ACID DURING THE DEVELOPMENT OF THE PEA

Certain quantities of a substance present in different plants or parts of plants, may be calculated in relation to the fresh weight or the dry weight. The dry weight of the plant is changed by assimilation, by dissimilation and by transport. The fresh weight, moreover, depends on the water content. When calculating the quantity of a substance present on a *basis per plant*, this is independent of water content and assimilation.

In this case, however, the *variability* of the plants or the parts of the plants must be taken into account. Therefore, we determined the quantity of niacin as an average out of a series of 20 plants. We had shown that with the rigorous selection of the seeds as well as of the plant material, this number of plants was sufficient to get constant results in parallel series.

We grew our plants on water cultures, because then the plants could be made more homogeneous, the roots more suitable for analysis, and it was easier to manipulate investigations with controlled feeding.

We determined the amount of niacin in the plant in several stages of the development, to get an impression of the niacin metabolism in the pea (fig. 3). The total amount of niacin increases rapidly during the development of the pea. It is interesting to note a slow increase of the niacin content in the first 3 weeks followed by a sharp increase thereafter. The plants with an age of 3 weeks are, therefore, most suitable for our investigations. These plants were about 15 cm long and the seventh or eighth leaf had just developed. The maximum amount of niacin reached in our plants was about 20 times the value of the beginning. The increase of the niacin content was relatively small. The increase with plants grown in soil can certainly be greater. The plants which we had grown in waterculture developed in a normal way indeed, but had filled out less than would have been the case in soil. The amount of niacin again decreases towards the end of the period of vegetation. From this it is concluded that niacin may be converted into other compounds than the phosphopyridine

nucleotides, which we determined with our method as niacin too. As will be established in further investigations, niacin proved to have been converted into trigonelline. Thus the curve is the resultant of the synthesis and the conversion of niacin.

Moreover, it is of importance to know the distribution of the niacin content present in the different parts of the plant. Therefore, we

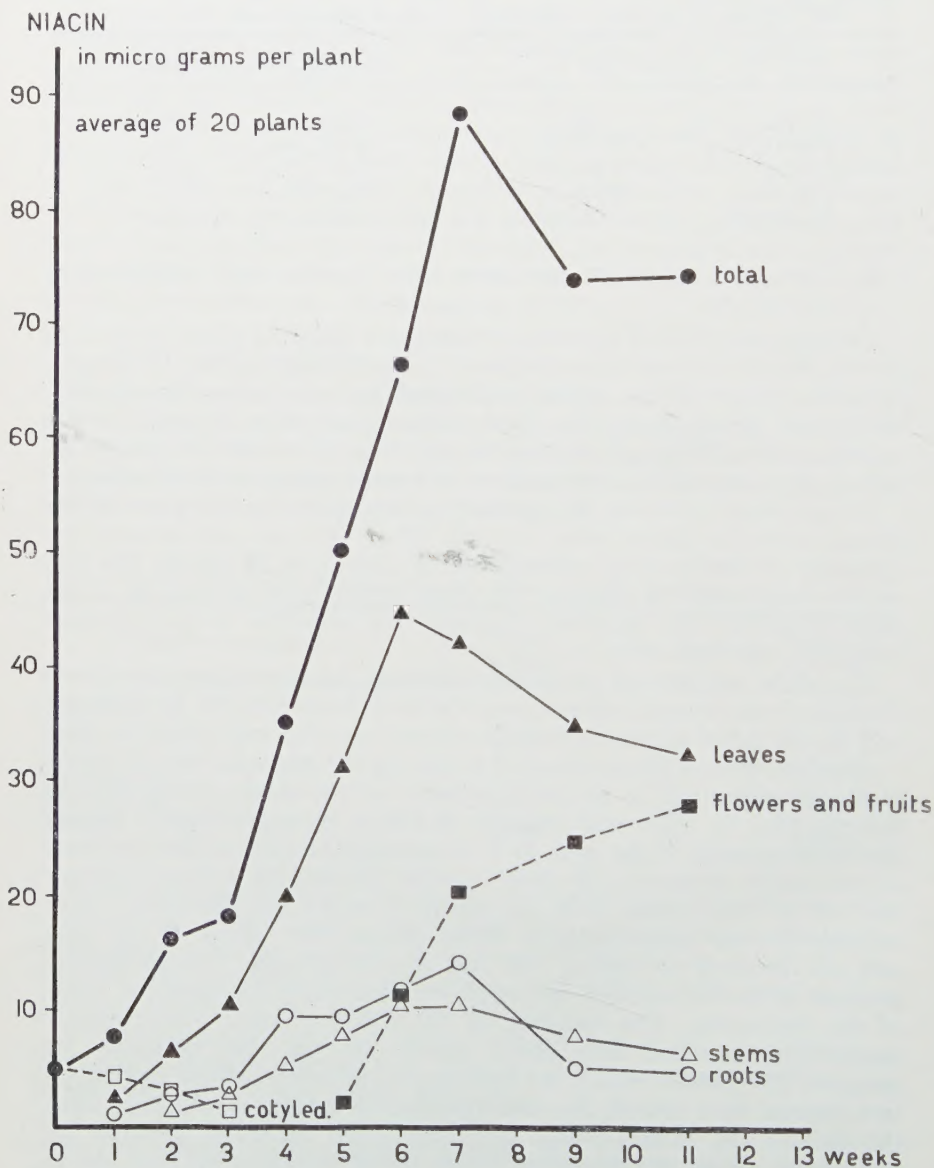


Fig. 3. The course of the nicotinic acid content in the green pea.

determined separately the quantity of niacin, both free and bound, present in the cotyledons, the roots, the stems, the leaves, the flowers and the fruits. The distribution of the amount of niacin over the various parts of the plant shows the following details (fig. 3). The quantity of niacin in the cotyledons decreases sharply, immediately after germination, whereas the quantity of niacin in the roots and leaves increases. Later on in the development of the plant after about 7 weeks, that is also the case with the roots, the stems and the leaves. In the niacin determination of the leaves those fallen off and dried were included. Although a conversion may appear at the same time it is noteworthy that this decrease takes place just at that time, when there is an increase of niacin in the fruits. So we presumed on good grounds that there is a *transport* in the seedling from the cotyledons into the other parts of the plant, and afterwards from the leaves into the fruits.

That there should appear a transport from the cotyledons into the seedling has also been shown in the experiments of BONNER (1938) in which isolated pea embryos could be grown *in vitro*, on condition that niacin was added as a growth-factor. Evidently the embryos of the normal plant obtain niacin from the cotyledons.

In other investigations it was shown that isolated pea roots in sterile culture cannot synthesize niacin (BONNER and DEVIRIAN 1939; ADDICOTT and DEVIRIAN 1939). So the increase of the niacin content we have shown in the roots is likely to be caused by a transport from higher parts of the plants. Whether such a transport really takes place, has not yet been established.

The sharp increase of the niacin content *in the leaves indicates an important synthesis*. This conclusion will be proved afterwards with the aid of cut plants.

§ 5. THE INFLUENCE OF EXTERNAL CIRCUMSTANCES ON THE METABOLISM OF NICOTINIC ACID

With a view to the experiments still to be described, in which different compounds are absorbed with the transpiration stream in cut plants, we examined *the influence of cutting* on the niacin metabolism of the plants. In cut plants the niacin metabolism may be disturbed, for the transport of compounds from the upper parts of the plant is eliminated.

In our experiments the stems were cut between the cotyledons and the first squamose leaves and placed in a 10 times diluted culture solution as indicated by HOAGLAND. These cut plants can be kept in good condition for several days. Further investigations, however, forced us to apply a shorter time for the experiment. An experiment lasting 3 days clearly showed that cut plants have the same niacin production as normal plants (table III, column 3). In both cases the increase of niacin amounts to 20 to 30 %. From this experiment we concluded that the niacin synthesis takes place in the leaves. For our further investigations *we can therefore use cut plants*.

Now we examined *the effect of light* on the production of niacin

(table III and IV). It appeared that in cut plants as well as in normal plants niacin is formed in the light, whereas in the dark no niacin is formed at all. Growth, however, was not inhibited in the dark. This does not include, of course, that the production of niacin itself would be a photochemical reaction. It is also possible that in the photo-

TABLE III

The influence of light and dark on the production of niacin in cut pea plants on a 10 × diluted culture solution. Niacin content calculated per plant as the average of the leaves of 20 plants.

Date of sowing	21/2	7/3
Beginning of the experiment	21/3	8/4
	Niacin in micrograms per plant	
Cut pea plants		
Beginning of the experiment	7	10
After 3 days in dark	7	—
After 3 days in light	—	13
Normal pea plants analyzed		
After 3 days	10	12

TABLE IV

The influence of light and dark on the production of niacin in normal pea plants. Niacin content calculated per plant as the average of 20 plants without roots.

Date of sowing	20/2	27/2	20/3
Beginning of the experiment	20/3	27/3	13/4
	Niacin in micrograms per plant		
Normal pea plants			
Beginning of the experiment	11	10	12
After 2 days in dark	10	11	11
After 2 days in light	—	13	14

synthesis compounds are formed which are indispensable for the synthesis of niacin.

The investigations of TERROINE and DESVEAUX-CHABROL (1947) also proved that niacin synthesis in *Phaseolus vulgaris* only takes place in the light.

The quantity of *nitrogenous* compounds which the plant has at its disposal, is obviously of great importance in the synthesis of niacin. When replacing, however, the culture solution of the water cultures by a nitrogen free solution, the production of niacin still proceeds for another couple of days. After about 5 days the plants show clear marks of lack of nitrogen. Then the lower leaves turn yellow, and the niacin content does not increase any further. It is not yet known, whether the synthesis of niacin is inhibited or whether the transformation is accelerated.

§ 6. THE TRANSFORMATION OF NICOTINIC ACID INTO TRIGONELLINE

It is well known that niacin is for the greater part used to synthesize the pyridine nucleotides. We have already pointed out that we estimated these compounds which are decomposed into niacin by hydrolysis, as the total amount of niacin present in the plant. For our further experiments it is necessary to investigate whether niacin can be converted into other compounds than those already mentioned. For this purpose a recorded quantity of niacin has to be absorbed by a plant. After some time we can analyse whether this quantity in the plant has decreased. If this is so, it has to be investigated by further analysis which compounds have been formed and which quantities are concerned with this process. In other words an attempt has to be made to draw up a *niacin balance*.

In order to make a series of 20 plants absorb a recorded quantity of a compound under controlled circumstances we constructed a new apparatus. The details of the construction are clearly shown in fig. 4. The level of the liquid is kept constant by an automatic siphon which is connected with the flask containing the stock-solution.

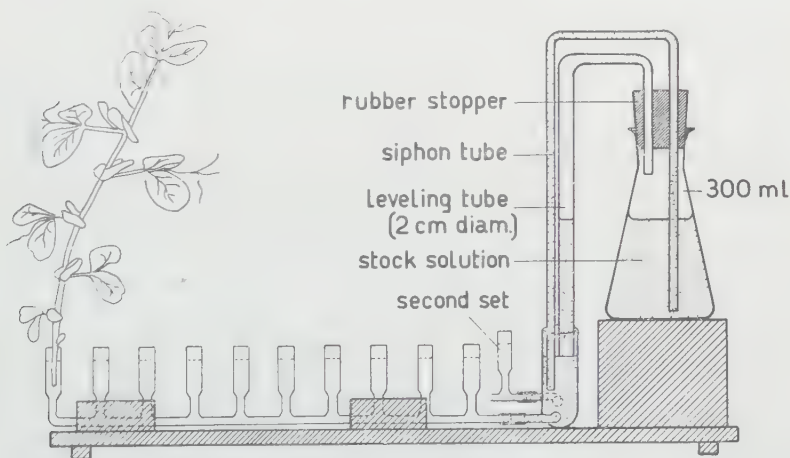


Fig. 4. The apparatus to feed cut plants with recordable quantities of the compounds to be investigated.

This apparatus proved to be very satisfactory in practice. All plants receive the same culture solution. During the experiment no culture solution has to be added. In this solution the compounds which are to be investigated may be dissolved. The quantity of the substance absorbed can be determined by weighing the apparatus before and after the experiment and from the concentration of the solution. The evaporation may be neglected, for during the experiment no change of the concentration in the liquid occurs. E.g. in one experiment a solution containing 18.4 microgram of niacin per ml was brought into the apparatus. After two days we determined 18.1 microgram of niacin per ml.

Now we made some series of plants absorb a recorded quantity of niacin, whereas parallel series were placed on the diluted culture solution only. After 2 days the plants were analysed to determine the niacin content. Table V shows that about 70 to 95 % of the niacin absorbed cannot be traced in the plant as niacin anymore and is consequently transformed by the plant. In this connection it may be remarked that important quantities of the niacin can be found back.

TABLE V

The conversion of niacin under different circumstances in cut pea plants. Niacin content calculated per plant in micrograms as an average of 20 plants. The experiment lasted 2 days.

Date of sowing	15/8	22/8	10/10	8/8	26/9	3/10
Beginning of the experiment	5/9	12/9	5/11	23/8	8/10	26/10
External circumstances	light	light	light	N-free	dark	dark
Pea plants without niacin added						
Leaves	9.5	9.4	—	6.7	—	—
Stem	2.1	2.7	—	2.3	—	—
Total	11.6	12.1	12.7	9.0	11.8	9.2
Niacin absorbed in 2 days.	100	55	107	45	171	81
Pea plant with niacin added						
Leaves	10.6	9.9	—	7.8	—	—
Stem	7.8	5.4	—	4.8	—	—
Total	18.4	15.3	37.9	12.6	65.2	29.2
Recovered niacin.	6.8	3.2	25.2	3.6	53.4	20.0
Lost in %.	93	94	76	92	69	75

This may be explained by the assumption that the transformation of the niacin occurs for the greater part in the leaves, whereas the stems of the cut plants could absorb niacin till the moment of analysis. Therefore, a part of the niacin absorbed will be found again unchanged in the stems.

In order to establish this fact accurately the leaves and the stems of some series were analysed separately. It appeared that although a large quantity of niacin was absorbed and brought to the leaves by the transpiration stream, the niacin content in the leaves remained practically constant. This points to a conversion of niacin in the leaves. The quantity of niacin recovered is for the greater part found in the stems. The increase of niacin in the stems is about 2 to 4 times the original quantity. This increase is probably due to the absorption of niacin for transport to the leaves.

The same experiments were made with normal plants in the dark and with plants lacking nitrogen in the light. The results were completely similar to those of the experiments already described (table V).

In a stage of development in which a distinct niacin synthesis takes place the plant is capable of converting large quantities of the niacin added.

For a long time now the hypothesis has been assumed that trigonelline could be formed from niacin. This, however, has not been proved satisfactorily. As was shown in the above mentioned experiments that an intensive niacin metabolism occurs in the plant the question arose whether trigonelline could be formed.

TABLE VI

The conversion of niacin into trigonelline in light with cut pea plants of an age of 3 weeks. Calculated per plant as an average of 20 plants.

	Niacin		Trigonelline		Total
	micro-grams	10 ⁻³ mmol	micro-grams	10 ⁻³ mmol	10 ⁻³ mmol
Beginning of the experiment . . .	12.7	0.10	179	1.31	1.41
Blank plant 2 days on a 10 × diluted culture solution					
A Found per plant.	16.6	0.13	237	1.73	1.86
Test plant 2 days on a 10 × diluted culture sol. with niacin					
B Absorbed per plant	301	2.45	—	—	2.45
C Found per plant.	103	0.84	484	3.53	4.37
Conversion C — (A + B)	— 215	— 1.74	+ 247	+ 1.80	+ 0.06

We investigated this in the way already described. Niacin was added to cut plants and the quantity absorbed was determined. Thereafter we analyzed the quantity of niacin and trigonelline present in these plants. These experiments also confirmed a strong conversion of niacin in the plant. Furthermore we could show a clear increase of the trigonelline content. As is shown in table VI the quantities of niacin and of trigonelline increase, too, in plants which were not fed with niacin. The total amount of niacin per plant does not change very much in this synthesis (from 12.7 to 16.6 micrograms), but the amount of trigonelline increases by 50 micrograms. In drawing up the balance we charged this synthesis by comparing the plant which had absorbed niacin for 2 days with the blank plants. The result was that 1.74×10^{-3} mmol of the niacin absorbed must have been converted and 1.80×10^{-3} mmol trigonelline has been formed. The difference is about 4 %, this is within the limits of error.

So we may conclude that in experiments over a short period *the conversion of niacin in the pea is limited practically to a production of trigonelline.*

This calculation is based on two suppositions. Firstly, the normal niacin synthesis in the pea is not influenced by the addition of a large amount of niacin. Secondly, all pyridine derivatives, belonging to the niacin group and taking part in the metabolism in plants, are determined in our chemical analyses either as niacin or as trigonelline.

These suppositions were justified when it was shown that the niacin balance squared. The blank plants contained 1.86×10^{-3} mmol pyridine derivatives (estimated as niacin and trigonelline); the test plants, which had absorbed 2.45×10^{-3} mmol niacin contained 4.37×10^{-3} mmol pyridine derivatives, whereas 4.31×10^{-3} mmol was calculated.

The purpose of our investigations was further to make researches into the niacin metabolism. As transformation of niacin into trigonelline appears to be so rapid, the trigonelline metabolism must be included. Therefore, besides the niacin determinations, trigonelline determinations have to be performed also. This necessity is particularly urgent because the niacin level of the plant under the normal physiological circumstances, retains a very constant value. This has been established in all our experiments.

§ 7. THE EFFECT OF SEVERAL COMPOUNDS ON THE PRODUCTION OF NICOTINIC ACID

It has become clear from the discussion of the literature on the subject that two groups of compounds are to be considered precursors in the synthesis of niacin. In the first place tryptophan and the compounds biochemically related with it e.g. kynurenine, kynurenic acid, 3-hydroxyanthranilic acid and quinolinic acid. The second group includes ornithine, citrulline and arginine.

In many experiments we investigated whether after the addition of dl-tryptophan or l-ornithine an increased synthesis of niacin or trigonelline could be obtained, with normal plants in the light. For this purpose we had solutions of these compounds absorbed by the transpiration stream into cut pea plants. After 2 days the niacin content and the trigonelline content of the test plants and the blanks were determined. We could not establish any increase of the niacin and trigonelline production either in plants of 2 weeks or in plants of 3 weeks old (table VII and VIII).

TABLE VII

The addition of ornithine and tryptophan to cut pea plants, aged about 2 weeks. Ornithine: 36.9 mg 1 (+) ornithine.2HCl dissolved in 500 ml diluted culture solution. Tryptophan: 33.1 mg dl-tryptophan dissolved in 500 ml diluted culture solution. Cut pea plants. Date of sowing 26/6. Beginning of the experiment 12/7. Calculated per plant as an average of 20 cut plants.

	Culture solution absorbed	Micrograms niacin	Micrograms trigonelline
Beginning of the experiment	—	7.7	149
Cut pea plants			
After 2 days on blank culture solution	8.7 ml	8.7	243
After 2 days and absorbed 675 μ g ornithine	9.2 ml	9.1	241
After 2 days and absorbed 622 μ g tryptophan	9.4 ml	9.0	239

These results agree with those of the investigations of TERROINE et al. (1948) and VOLGANI and SNELL (1948). Our results do not correspond with those of GUSTAFSON (1949), NASON (1949-50) and BANERJEE *et al.* (1950).

In accordance with the method described we further examined the effect of pyridoxine and pyruvic acid on the production of niacin

TABLE VIII

The addition of ornithine and tryptophan to cut pea plants, aged about 3 weeks. Ornithine: 103.3 mg 1 (+) ornithine.2HCl dissolved in 500 ml diluted culture solution. Tryptophan: 100.6 mg dl-tryptophan dissolved in 500 ml diluted culture solution. Cut pea plants. Calculated per plant as an average of 20 plants. Date of sowing 31/7. Beginning of the experiment 21/8.

	Culture solution absorbed	Micrograms niacin	Micrograms trigonelline
Cut pea plants after 2 days			
in blank culture solution	8.5 ml	13.7	262
absorbed 2.53 mg ornithine . . .	12.3 ml	12.5	209
absorbed 1.58 mg tryptophan . .	7.9 ml	12.0	256

and trigonelline in the pea. These compounds were tested separately and in combination with tryptophan, ornithine and citrulline (table IX and X). In some experiments the addition of vitamin B₆, pyruvic acid and ornithine caused indeed a small increase of about 15 % of the trigonelline content, whereas the amount of niacin remained constant. But these results were not found in all our experiments. This is in agreement with the investigations of NASON (1949).

TABLE IX

The addition of citrulline and pyridoxine to cut pea plants. Citrulline: 22.2 mg 1 (+) citrulline dissolved in 500 ml diluted culture solution. Pyridoxine: 25.3 mg dissolved in 500 ml diluted culture solution. The combination contained: 21.6 mg 1 (+) citrulline and 26.0 mg pyridoxine dissolved in 500 ml diluted culture solution. Cut pea plants of 3 weeks age, in the light. Calculated per plant as an average of 20 plants.

	Culture solution absorbed	Micrograms niacin	Micrograms trigonelline
Cut pea plants after 2 days			
in blank culture solution	10.5 ml	13.3	271
absorbed 404 μ g citrulline. . . .	10.4 ml	13.9	241
absorbed 524 μ g pyridoxine . . .	9.8 ml	13.6	268
absorbed 421 μ g citrulline and 507 μ g pyridoxine	9.1 ml	14.2	268

The niacin synthesis was totally inhibited almost directly by putting the plants in the dark, as was shown in par. 5. It may be assumed for experiments lasting a short time that the enzyme system is still present and entirely intact. There must then be a lack of an essential product. We fed plants with ornithine in the dark, but could not

show an increased niacin or trigonelline production (table XI). A drawback of the experiments in the dark, however, is the etiolation of the plants.

Furthermore niacin synthesis is inhibited by a lack of nitrogenous compounds. To obtain nitrogen deficient plants they must be grown under these circumstances for a longer period. Then the objection

TABLE X

The addition of ornithine or tryptophan together with pyridoxine and pyruvic acid to cut pea plants. Solution B: 45.1 mg l (+) ornithine.2HCl, 48.0 mg pyridoxine and 135 mg pyruvic acid dissolved in 1 liter diluted culture solution. Solution: C: 23.10 mg dl-tryptophan; 21.8 mg pyridoxine and 69.2 mg pyruvic acid dissolved in 500 ml diluted culture solution. Cut pea plants of 3 weeks age, in the light.

Calculated per plant as an average of 20 cut pea plants.

	Culture solution absorbed	Micrograms niacin	Micrograms trigonelline
Cut plants after 2 days			
A in blank culture solution	11.8 ml	15.7	270
B absorbed 571 μ g ornithine 607 μ g pyridoxine and 1708 μ g pyruvic acid .	12.8 ml	15.1	274
C absorbed 647 μ g tryptophan 610 μ g pyridoxine and 1938 μ g pyruvic acid .	14.0 ml	14.1	274

TABLE XI

The addition of ornithine to cut pea plants in the dark. Ornithine: 34.8 mg l (+) ornithine.2HCl dissolved in 500 ml diluted culture solution. Cut pea plants aged 3 weeks. Experiment in the dark. Calculated per plant as an average of 20 plants.

	Culture solution absorbed	Micrograms niacin	Micrograms trigonelline
Beginning of the experiment		22	319
Cut plants in 2 days in the dark			
in blank culture solution	12.8 ml	21	292
absorbed 863 μ g ornithine	12.4 ml	20	246

can be made that the enzyme systems are influenced. Moreover, the compounds added are, at least for the greater part, very probably converted, first into other substances, which are necessary for the plant. Although these experiments are of less importance in relation to our problem, yet we performed a few experiments with plants lacking nitrogenous compounds. Such plants we fed ornithine, citrulline or tryptophan in combination with pyridoxine and pyruvic acid. We could not show any increase of the amount of niacin and trigonelline (table XII).

Therefore we must conclude that none of the compounds examined determine the rate of the niacin production under the circumstances investigated.

TABLE XII

The addition of ornithine or tryptophan to cut pea plants with a lack of nitrogenous compounds. Ornithine: 107.3 mg l (+) ornithine.2HCl dissolved in 500 ml diluted culture solution. Tryptophan: 103.5 mg dl-tryptophan dissolved in 500 ml diluted culture solution. Pea plants with a clear lack of nitrogen. Experiment in the light. Calculated per plant as an average of 20 plants.

	Culture solution absorbed	Micrograms niacin	Micrograms trigonelline
Beginning of the experiment	—	9.8	235
Cut pea plants after 2 days			
in blank culture solution	11.2 ml	—	290
absorbed 2.55 mg ornithine	12.4 ml	—	275
absorbed 2.32 mg tryptophan . . .	13.5 ml	10.8	253

§ 8. SUMMARY

1. An active nicotinic acid metabolism has been established during the development of the green pea (fig. 3).

2. The nicotinic acid production was inhibited by putting the plants in the dark or when the plants lack nitrogenous compounds.

3. We constructed an apparatus with which it was possible to determine in a simple way the amount of a substance absorbed by cut plants (fig. 4).

4. Cut pea plants were proved to have a normal nicotinic acid synthesis, therefore the leaves were supposed to synthesize nicotinic acid.

5. Above a definite level the nicotinic acid absorbed by the leaves is quantitatively transformed into trigonelline.

6. The balance-sheet of niacin was drawn up (table VI). From this we concluded that all pyridine compounds which take part in metabolism, are determined in our analyses, either as trigonelline or as nicotinic acid.

7. The nicotinic acid level of the pea retains a very constant value under normal physiological circumstances.

8. The addition of tryptophan, ornithine, citrulline, pyridoxine and pyruvic acid separately or in combination did not cause any increase of the nicotinic acid or trigonelline content.

9. The addition of tryptophan or ornithine with nitrogen free plants and of ornithine with plants in the dark gave the same results.

10. Therefore we concluded that the compounds mentioned above did not determine the rate of the nicotinic acid synthesis.

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A MONOGRAPH OF THE VOCHYSIACEAE III. QUALEA¹

BY

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The genus *Qualea* is found in tropical South America, particularly in the Hylaea and in the Extra Amazonian part of the Brazilian mainland (see fig. 3); it comprises 59 species as defined in this paper. Many species are forest trees occurring in the Amazonian basin, a number are found in the Brazilian Atlantic coastal forests, whereas other species are typical trees of the campos of the interior plateau.

The genus was first described by AUBLET in 1775; its name is a latinization of the vernacular name "Qualé" used by the "caribbean" inhabitants of French Guiana. AUBLET described *Q. rosea* (type species) and *Q. coerulea*; the first exhaustive and morphologically correct description was given by A. DE ST. HILAIRE (1820) who placed the genus in his newly established family of the *Vochysiaceae*.

ACKNOWLEDGMENTS

The continuation of the revision of the *Vochysiaceae* has been made possible by the courtesy and the co-operation of the herbaria and institutions listed in the second part of this monograph. The author wishes to express once again his sincerest thanks to the directors of these institutions who placed their very important collections at his disposal in such a courteous and generous manner. He had the opportunity of visiting the herbaria in Leiden, London (British Museum of Natural History) and Paris; while it was his privilege to accomplish his task at the Utrecht Botanical Museum. His grateful acknowledgments go to the directors and staff of these herbaria; their great help and kind hospitality were of great value to him.

The abbreviations for the herbaria used in this publication are those proposed in the Index Herbariorum of the International Association for Plant Taxonomy (see LANJOUW et STAFLEU 1952).

¹ Part I, (*Salvertia* and *Vochysia*) in Rec. Trav. Bot. Néerl. **41**: 397–540, 1948; also in Med. Bot. Mus. Utr. **95**: 397–540.

Part II (*Callisthene*) in Acta Bot. Néerl. **1**: 222–242, 1952; also in Med. Bot. Mus. Utrecht **108**: 222–242, 1952.

MORPHOLOGICAL REMARKS

Qualea constitutes with the genera *Salvertia*, *Vochysia* and *Callisthene* the tribe of the *Vochysieae* Dumort. (1829 p. 6).

The comparative morphology of these genera was discussed in some detail in the second part of this monograph. The following remarks are mainly concerned with the variation within the genus *Qualea*¹.

The diagrams of the flowers of some species of *Qualea* are given in fig. 1. Not every type of flower which may be encountered in this genus is represented in this figure: the variable number of staminodes

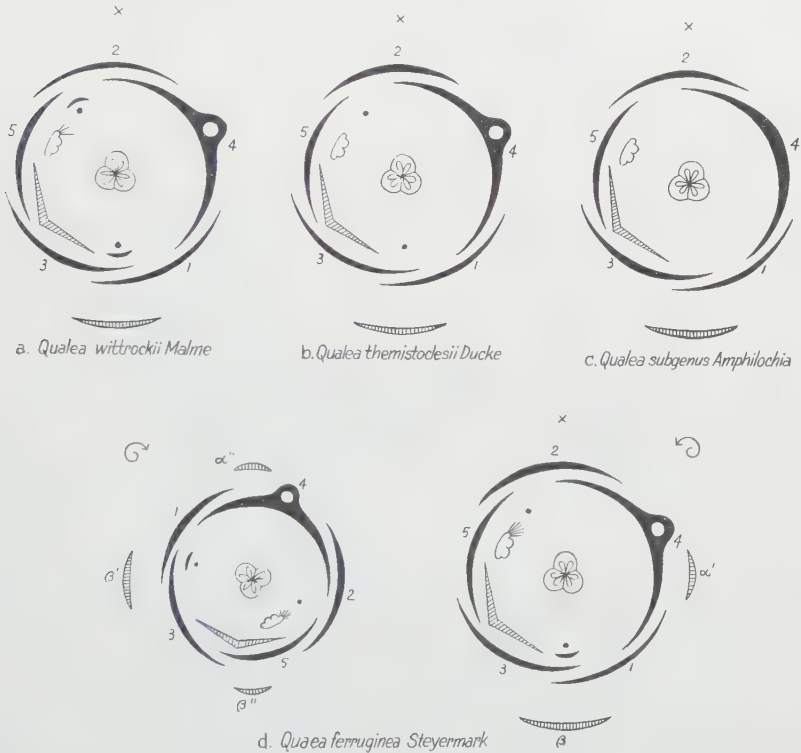


Fig. 1. Diagrams.

and rudimentary petals, together with the presence or absence of a unilateral indumentum on the stamen provide many possibilities.

A. Calyx. In the subgenus *Qualea* the fourth and major lobe of the calyx is provided with a distinct spur; this spur is absent in the subgenus *Amphilochia*. Apart from this presence or absence of a spur two types of calyx may be distinguished:

I. The *Vochysia* type (see e.g. fig. 4c). The fourth (spurred) lobe is three or more times longer and always much wider than the other lobes. The latter are closely adpressed against the former. This type

¹ The subdivision of the genus *Qualea* is given on p. 152.

of calyx is found in *Vochysia* and *Callisthene*, and in *Qualea* sect. *Trichanthera*.

II. The *Salvertia* type. (see e.g. fig. 13d). The fourth (spurred) lobe is about as large as the other lobes; the latter are never closely adpressed against the former. This type is found in *Salvertia*, *Erisma* and *Erismadelphus*; in *Qualea* it is found in all species except in those belonging to the section *Trichanthera*.

B. The Corolla consists of one well developed petal, sometimes flanked by one or two rudimentary ones (see fig. 1). This petal of *Qualea* — like the central petal of *Vochysia* — corresponds to the third petal of *Salvertia* (see diagrams in STAFLEU 1952 p. 224). In the subgenus *Qualea* small rudimentary petals may occasionally be found in the same positions as the lateral petals of *Vochysia*. In this latter genus the lateral petals are only rarely reduced or absent; in *Qualea* this is the rule.

It is often difficult to decide whether organs found in this position are staminodes or petals: the staminodes in *Qualea* (and in *Vochysia*) belong to the second cycle of stamens situated at the base of the petals. Only when both kinds of organs are present is it evident that the flimsy straps flanking the main petal do indeed represent the lateral petals (the numbers 1 and 5 of the theoretical cycle).

C. Androecium. The only fertile stamen stands in front of the first calyx-lobe outside the plane of symmetry; it therefore belongs to a cycle alternating with the corolla. The staminodes (0, 1, 2, or 3) always belong to a second — alternating — cycle.

In different flowers of one species and even of one specimen the number of staminodes may vary and as this is also true of the rudimentary petals it is evident that many different combinations may be seen. These types have only slight taxonomic value: the most complete flowers are found in the section *Trichanthera*; some of the species of sect. *Qualea* and sect. *Costatifolium* are also provided with rudimentary organs, but in the section *Polytrias* and in the subgenus *Amphilochia* none are found.

Two types of fertile stamen may be distinguished:

1. *Innate* (also in *Salvertia*, *Vochysia* and *Callisthene*). In *Qualea* stamens of this type occur in the section *Trichanthera* in which they are provided with a unilateral beard (cf. fig. 1a and 8d).
2. *Dorsifixed* (also in *Erisma* and *Erismadelphus*). All other species of *Qualea* have stamens of this type: the filament is attached either to the centre of the connective (sect. *Costatifolium*) or somewhat above the base of the back (fig. 12c and 13c).

D. Stipules. One of the main peculiarities of *Qualea* is the manifold specialization of the stipules. They provide characters which are of great importance for the determination of sterile specimens. This usefulness is enhanced by the fact that the specializations are generally characteristic of the species concerned.

a. Glands. The following types may be distinguished:

1. *Transformed stipules* (see fig. 2 and 7). The stipules are fully developed; the apex is short and often deciduous or caducous; the base is

glandular. This base may be swollen in youth (fig. 2) and even remain so for its life time, but more often it is transformed into a crateriform "gland" which is rather flat, elliptic or round and provided with a thick-walled often light-coloured margin (see fig. 7).

Only a careful anatomical investigation of duly conserved materia

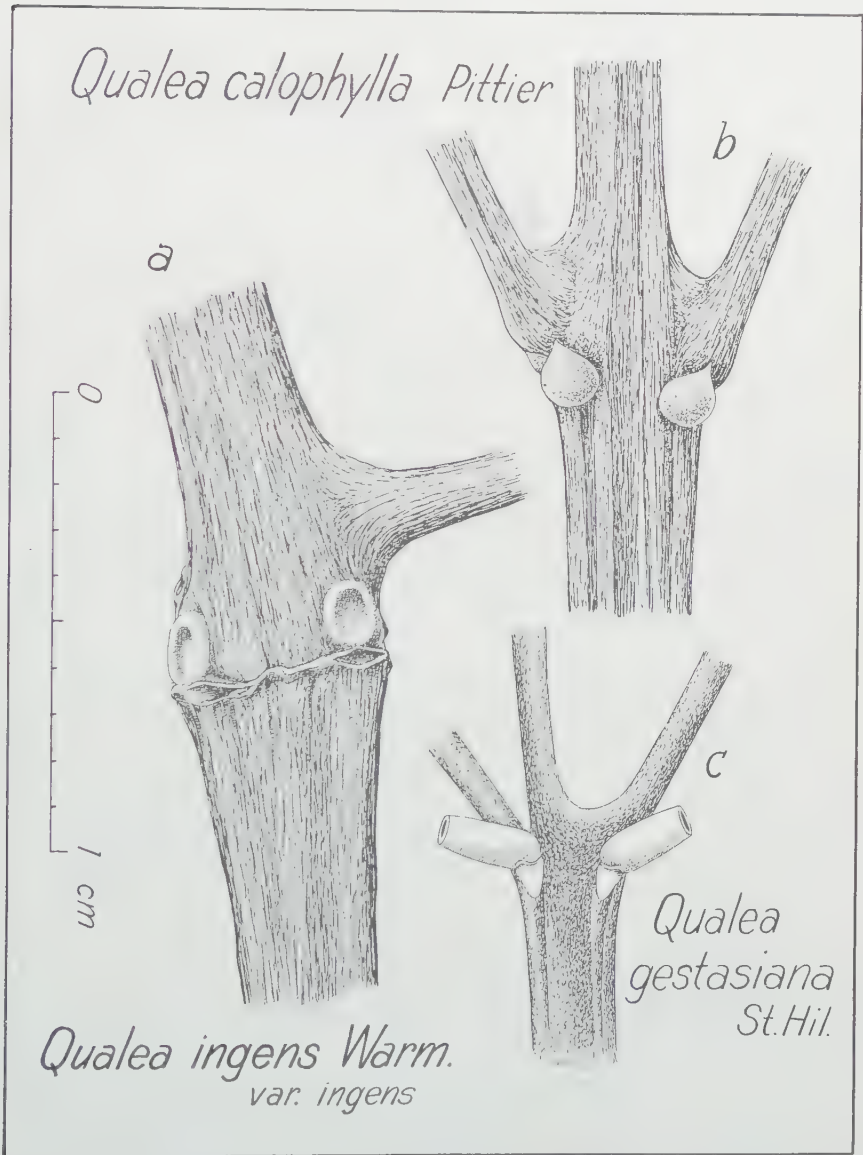


Fig. 2. Glands in the genus *Qualea*. a. Axillary glands; b. young transformed stipules; c. true extrafloral nectaries.

would make it clear whether the inside of these "glands" is indeed glandular.

This type of gland is present in quite a number of species from all groups, e.g. *Q. calophylla*, *Q. rigida*, *Q. grandiflora*, *Q. tessmannii*.

2. *Stipular glands* (fig. 4 and 9). The stipules are represented by the crateriform glands described above. The apex is absent. This type is found in most species.

3. *Axillary glands* (fig. 2 and 10). The stipules are complete, either flat or incrassate. In their axils glands are found which show a great resemblance to those of the first two types. In some cases, however, (fig. 10) they are subglobose with a narrow mouth. All are provided with a thick callous margin or wall. Glands of this type are found in e.g.: *Q. ingens*, *Q. lineata*, *Q. glaziovii* (see POULSEN 1876 p. 273), *Q. elegans* (glands in serial pairs).

4. *True extrafloral nectaries*. POULSEN (1881) has demonstrated with pickled material that the structures as depicted in our fig. 2 are indeed extrafloral nectaries. These are tube-shaped (in other cases subglobose or urceolar), thin-walled nectaries, situated in the axils of the stipules. Here too the bases of the stipules may be either flat or incrassate (subglandular). Such nectaries are found in *Q. gestasiana*, *Q. amoena*, *Q. magna*, *Q. paraensis* and *Q. rosea*.

b. The "stipular ridge". Sometimes the stipules of opposite leaves are connected by a narrow transverse elevated line. This ridge merges into the bases of the stipules. It is interesting to make a comparison with the situation found in the *Trigoniaceae* where the stipules are often interpetiolar and at the same time not connate.

E. The vegetative buds of *Qualea* are very often perulate, that is, furnished with a number of small protective scales (see also part II p. 225). As in *Callisthene*, these scales or cataphyls, are more or less persistent and they are to be found at the bases of the young branchlets. The basal ones are crowded and the respective internodes are correspondingly short. This is especially so in species of the subgenus *Amphilochia*.

F. The inflorescence — as always in this family (see part II p. 226) — is characterized by the cincinnus (fig. 1e). It is therefore remarkable that *Q. cymulosa*, the only Central American species of the genus, has a panicle of distinctly peduncled three-flowered regular cymes. This feature separates this already geographically isolated species from all others.

GEOBOTANICAL AND ECOLOGICAL REMARKS

The area of *Qualea* is continuous, as can be seen from fig. 3. It lies in tropical South America but it has a very slight extension towards Panama where the morphologically isolated species *Q. cymulosa* is found. In South America the area nearly covers that of *Vochysia* with the exception of an extension into the northern Venezuelan mountains (*Q. calophylla*). For a discussion of the boundaries of this area see part I p. 409–414.

The western boundary of *Qualea* runs along the eastern slopes of

the Andes. Unlike *Vochysia* the species are not found in the subtropical parts of these mountains. The southern boundary follows the 18° isotherm of the coldest month, which may be used for the delimitation of the tropical zone. In eastern Brazil several endemic species are found in the atlantic coastal forests. The northern boundary follows the coastline except in the extreme East where *Qualea* is absent in Parahyba and northern Ceara and in the extreme West, where it avoids the dry coastal parts of Venezuela.

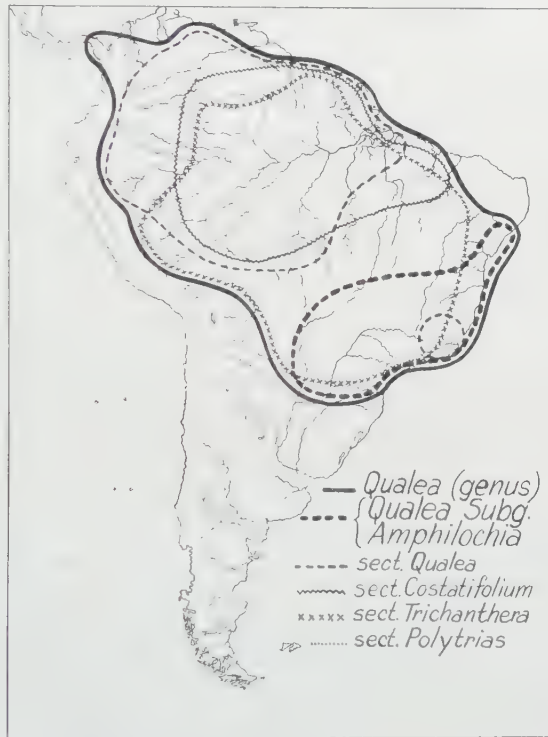


Fig. 3. Distribution of the genus *Qualea* and its subdivisions.

The species of *Qualea* — like those of *Vochysia* — are found either in the rain forests or in the savannas (campos and llanos). Some species are present in the Caatinga and the Cacaes zones of Brazil (see SAMPAIO 1934) but in these zones they are found in places which can be considered as “disjunctions” of the zone of the campos. This is also the case with the occurrence of *Q. grandiflora* and *Q. parviflora* — both typical trees of the campos — in the Hylaea.

The areas of the subgenera and sections have been indicated in fig. 2. The section *Qualea* has a disjunct area: the major part of the species is Hylaeen, whereas three species are southern Brazilian. Two of the latter are trees of the coastal rain forests, one is a shrub of the

campos. The disjunction Hylaea-Coastal Forests may be encountered in many taxa, in the *Vochysiaceae*, for instance, in *Vochysia* subsect. *Ferrugineae*.

In general it may be said that the subgenus *Amphilochia* is restricted to the zones of the Campos and of the Coastal Forests. The sections *Trichanthera* and *Qualea* are chiefly Hylaeae. The species of the section *Costatifolium* are found either in the Hylaea or in the Campos, with "disjunctions" into the neighbouring zones.

NOTES AND ABBREVIATIONS

Most of the species of *Qualea* are of very little economic value or even of no use at all. A number of rain forest species are in use as timber or lumber trees but for the most part the products seem to be of moderate or even of inferior quality.

Several "kwarrie" species are included among wood from Suriname used in the Netherlands for industrial purposes (*Q. albiflora*, *Q. rosea*, *Q. dinizii* and *Q. coerulea*).

ST. HILAIRE (1820 p. 261) relates that the inhabitants of Minas Geraes used to extract a dye from the cortex of "pau terra" (*Q. grandiflora*, *Q. multiflora* and *Q. parviflora*).

The abbreviations used for the herbaria are those proposed in the Index Herbariorum (LANJOUW et STAFLEU 1952).

Fl. Months during which flowering specimens have been collected.

Fr. Idem, fruiting specimens.

s.n. unnumbered specimen.

Qualea Aubl.

Aubl. Pl. Gui. 1: 5. 1775; Juss. 1789 p. 424; Lam. 1791 p. 11; Willd. 1797 p. 18; Poir. 1804 p. 8; Vahl 1804 p. 6; Roem. & Schult. 1817 p. 5; St. Hil. 1820 p. 253, 265, 269; Mart. 1824 p. 130; Spreng. 1825 p. 4, — 1827 p. 4; DC. 1828 p. 28; A. Dietr. 1831 p. 97; Meisn. 1836-43 1: 119, 2: 85; Endl. 1836-40 p. 1178; D. Dietr. 1839 p. 21; Steud. 1841 p. 425; Benth. & Hook. 1862-67 1: 976; Baill. 1874 p. 95; Warm. 1875 p. 29; Petersen 1896 p. 317; Record and Moll 1924 p. 366; Benoist 1915 p. 237, — 1931 p. 163; Lemée 1934 p. 709; Record and Hess 1944 p. 551; Mennega 1948 p. 44; Staf. 1951 p. 190, — 1952 p. 223 seq. *Amphilochia* Mart. 1824 p. 127; Spreng. 1827 p. 4; DC. 1828 p. 26; G. Don 1832 p. 669; Meisn. 1836-43 1: 119, 2: 85, 355; Endl. 1836-40 p. 1177; D. Dietr. 1839 p. 21; A. Dietr. 1831 p. 96; Spreng. 1830 p. 21. *Agardhia* Spreng. 1825 p. 4, 17; DC. 1828 p. 30; A. Dietr. 1831 p. 97. *Schuchia* Endl. 1836-40 p. 1178; Walp. 1843 p. 68.

Trees or shrubs. Indumentum, if present, consisting of simple or biramose hairs. Perulate buds often present. Stipules often represented by crateriform glands, sometimes normally developed and provided with similar axillary glands or with extrafloral nectaries. Leaves opposite, simple, petioled, entire, coriaceous or subcoriaceous, penninerved, equal-sided or nearly so, the petioles mostly rugulose and

canaliculate above, the midrib prominent below. Flowers either solitary or in few-flowered cincinni in the axils of the leaves or in the terminal and axillary compound racemes or panicles with cincinni (very rarely regular cymes) as partial inflorescences, hermaphrodite, irregular. Bracts caducous. Peduncles extremely short. Pedicels distinct. Calyx gamosepalous, quincuncial, the base cup-shaped, the limb five parted, the lobes unequal and deciduous: the fourth ("posterior", "major" or "spurred") one large, mostly spurred or bag-shaped at the base, convolute and enveloping the inner whorls; the other lobes varying in size but always smaller, the second one on the axial side, the first and second ("lateral") ones often smaller than the third and fifth ("anterior") ones; spur, if present, at first adpressed against the back of the lobes, later on patent. Corolla white, yellowish, yellow, purplish-blue or pink, often spotted with violet, with the stamen and the staminodes perigynously inserted on the calyx. Petal one, membranous, alternating with the third and fifth calyx-lobes, convolute, caducous, generally obcordate, the base unguiculate. Rudimentary petals sometimes present. Stamen one, in front of the fifth calyx-lobe; the filament in anthesis often elongated, the anther bithecate, the locules introrse, adhering to the filament at the base (innate), somewhat above the base or in the centre (dorsifixed); the connective not or slightly produced beyond the locules; the pollen grains globose, triporous. Staminodes often present, glabrous, small. Pistil tricarpellary. Ovary superior, densely pilose, trilocular, the outer wall trisulcate, dissepiments complete; the ovules up to 12 per loculus, inserted in two rows, axile, epitropous, integuments two. Style one, simple, in anthesis often elongated and spirally coiled. Stigma one, terminal, mostly subcapitate. Fruit a trilocular loculicidal capsule, mostly shortly cylindric, the angles rounded or obtuse, never winged; the exocarp thick, woody, mostly adhering to the thinner endocarp, central column if present free and thin or breaking away with the valves. Seeds exalbuminous, few per loculus, oblong, winged, the wing unilateral, consisting of numerous long hairs inserted on the chartaceous testa, the body of the seed tomentose. Embryo homotropous, straight; radicle small, the cotyledons convolute and plicate.

Type species: *Qualea rosea* Aubl.

Distribution: 59 species in tropical America.

Ecology: Mostly trees of rain forests or savannas.

Remarks on the subdivision: MARTIUS (1824) described the genus *Amphilochia* as distinct from *Qualea*. WARMING (1875), however, gave this taxon the rank of "series", whereas in this monograph it is considered to be of the rank of subgenus. MARTIUS had good reasons to establish a separate genus: the species concerned differ from those of the present subgenus *Qualea* by a number of important characters such as the absence of a spur, a thick, densely pilose petal, the complete absence of staminodes. Yet the differences existing between the other genera of the *Vochysiaceae* tribe *Vochysieae* are of greater importance: the stamen may belong to another cycle (*Vochysia*, *Salvertia*), the structure of the capsule may be fundamentally different (*Callisthene*), etc. Intermediate forms between the present genera are never observed. The characters dividing *Amphilochia* and *Qualea* are not as "absolute" as those dividing these present genera; for instance, a non-spurred calyx is found in *Q. calantha* (subgenus *Qualea*), a more or less membranous petal in *Q. lundii* (subgenus *Amphilochia*), etc. For these reasons the present author does not wish

to reinstate *Amphilochia* as a genus. A secondary but nevertheless very important reason is found in the circumstance that he thinks it unfit, without very convincing arguments, to effect changes in generic names which would necessitate the re-naming of several common species. WARMING's concept of a series differs somewhat from that of our days: it is not certain whether he considered to category "series" to be higher or lower in rank than "section". In his treatment of the Brazilian species of *Qualea*, WARMING (1875) distinguished three series: *Calophylloideae*, *Costatae* and the above-mentioned *Amphilochia*. The first two series cover our present subgenus *Qualea*. In this monograph this latter subgenus is divided into four sections. In order to be in agreement with Art. 31 of the "Code", the names of these sections are substantives resembling the names of genera. This makes it inadvisable to use WARMING's names again (they have of course no status outside the rank of series). WARMING's first series (*Calophylloideae*) is more or less covered by our sections *Trichanthera* and *Qualea*, his second series (*Costatae*) is about covered by our *Costatifolium*. Our fourth section (*Polytrias*) contains only one species, unknown to WARMING.

This division of the subgenus *Qualea* into four taxa of equal rank seems justified in the light of the present knowledge of the variation in the subgenus. The section *Trichanthera* is well characterized by its innate, barbate anther and "Vochysioid" calyx, the section *Costatifolium* by its peculiar leaves and perulate buds (both absent in the former and following sections), and the section *Polytrias* by its cymes (absent in all other sections).

Key to the subgenera and sections

- 1a. Petal glabrous or nearly so; spur clavate or cylindrical, well developed. subgenus I. **Qualea** 2
- b. Petal densely pilose. Spur not or very weakly developed: the base of the fourth calyx-lobe shallowly saccate or gibbous subgenus II. **Amphilochia** (Mart.) Stapf. p. 202.
- 2a. Lateral nerves 10–50 per cm, making an angle of about 80' with the midrib 3
- b. Lateral nerves 8 or less per cm (major ones), making an angle of 60–80' with the midrib 4
- 3a. Anther unilaterally barbate. Spurred calyx-lobe 3 or more times longer than the other lobes, the latter closely adpressed against the former sect. A. **Trichanthera** Stapf. p. 153.
- b. Anther glabrous or pilose on the back. Spurred calyx-lobe somewhat longer than or at most up to $2\frac{1}{2}$ times longer than the other lobes, the latter never closely adpressed against the former sect. B. **Qualea** p. 170.
- 4a. Inflorescence composed of cincinni sect. C. **Costatifolium** Stapf. p. 192.
- b. Inflorescence a panicle of regular trichotomous peduncled cymes sect. D. **Polytrias** Stapf. p. 201.

subgenus I. **QUALEA**

Arbores vel frutices. Folia nervis lateralibus numerosis vel satis paucis, rectis et exacte parallelis, nervo limbalis margini proximo parallelo junctis. Calcar calycis clavatum vel cylindricum primum dorso laciniae adpressum, dein patens. Petalum glabrum vel fere glabrum, tenerum.

Type species: *Qualea rosea* Aubl. (type species of genus).

Distribution: 51 Species, widely distributed in the Hylaea Americana and

in the Extra Amazonian Province of Brazil with the adjacent parts of Bolivia and Northern Paraguay.

Section A. **Trichanthera** Staffl. nov. sect.

Series I *Calophylloideae* Warm. 1875 p. 30 p.p.

Arbores vel frutices. Perulae perpaucae.

Folia glaberrima basi haud obliqua, nervis lateralibus numerosissimis (5–50 per cm.) parallelis sub angulo c. 80° e costa ortis nervo limbali margini parallelo et proximo $\frac{1}{2}$ –1 mm) junctis. Alabastra elongato-conica. Calycis lacinia quarta calcarata, ceteras arte adpressas pluries superans. Anthera unilateraliter barbata, innata, filamento glabro. Stamina et petala rudimentaria saepe adsunt. Ovarium in stylum sensim transiens (exc. *Q. cassiquiarensis*).

Type species: *Qualea trichanthera* Spruce ex Warm.

Distribution: 15 Species of Hylaea and 1 of Caatinga.

Key to the species

- | | |
|--|---|
| 1a. Leaves glabrous or nearly so. | 2 |
| b. Lower surface of young leaves conspicuously ferrugineous-tomentellous | 1. Q. rubiginosa Staffl. |
| 2a. Apex of the leaves acute-acuminate. | 3 |
| b. Apex of the leaves rounded or obtuse and often retuse or shortly obtuse-acuminate. | 6 |
| 3a. Spur about as long as or somewhat longer than the pedicel, rarely only slightly shorter | 4 |
| b. Spur distinctly shorter than the pedicel, mostly about half as long | 2. Q. trichanthera Spruce ex Warm. |
| 4a. Basal half or two-third of the style densely hirsute | 5 |
| b. Style glabrous except the basal 1–3 mm | 3. Q. clavata Staffl. |
| 5a. Leaves ovate or ovate-elliptic, $1\frac{1}{2}$ –2 times longer than wide | 4. Q. gardneriana Warm. |
| b. Leaves oblong-lanceolate or subelliptic-oblong, $2\frac{1}{2}$ –4 times longer than wide | 5. Q. wittrockii Malme |
| 6a. Flowers in the axils of frondose leaves only, no terminal inflorescences | 7 |
| b. Flowers arranged in terminal — often branched — inflorescences, only the lowermost flowers or cincinni in the axils of the upper leaves | 8 |
| 7a. Cortex of the branchlets exfoliating (small fragments). | 6. Q. retusa Spruce ex Warm. |
| b. Cortex of the branchlets not exfoliating | 7. Q. albiflora Warm. |
| 8a. Leaves thinly coriaceous. | 9 |
| b. Leaves firm, thick and leathery | 11 |
| 9a. Leaves about two times longer than wide | 7. Q. albiflora Warm. |
| b. Leaves about three to four times longer than wide | 10 |

- 10a. Petioles 2–4 mm long. Cortex not exfoliating 8. **Q. nitida** Staff.
 b. Petioles 6–10 mm long. Cortex exfoliating (small fragments)
 15. **Q. urceolata** Staff.
- 11a. Base of the leaves rounded or cordate 12
 b. Base of the leaves cuneate or obtuse 14
- 12a. Leaves about two times longer than wide 13
 b. Leaves about three times longer than wide, $8-11 \times 2\frac{1}{2}-4$
 cm 9. **Q. rigida** Staff.
- 13a. Leaves $5-6 \times 2\frac{1}{2}-3\frac{1}{2}$ cm 10. **Q. verruculosa** Staff.
 b. Leaves $7-10 \times 3-5\frac{1}{2}$ cm. 11. **Q. esmeraldae** Standl.
- 14a. Flower-buds 2–4 mm wide near the base; spur distinctly
 longer than wide 15
 b. Flower-buds 5–6 mm wide near the base; spur bag-shaped,
 $3-4 \times 3-4$ mm 12. **Q. cassiquiarensis** Spruce ex Warm.
- 15a. Flower-buds fulvous-puberulous or nearly glabrous. Style
 glabrous except the lower 1–5 mm. 17
 b. Flower-buds ferrugineous-pubescent. Style ferrugineous-
 hirtous on the lower $\frac{2}{3}$ part 16
- 16a. Spur clavate; leaves $10-13 \times 4\frac{1}{2}-6$ cm 13. **Q. belemnensis** Staff.
 b. Spur cylindrical; leaves $5-9 \times 2\frac{1}{2}-4\frac{1}{2}$ cm 14. **Q. ferruginea** Steyermark
- 17a. Spur conspicuously clavate 18
 b. Spur subcylindrical, 4–7 mm long, about as long as or
 somewhat shorter than the pedicel 19
- 18a. Spur shorter than the pedicel 15. **Q. urceolata** Staff.
 b. Spur longer than the pedicel 3. **Q. clavata** Staff.
- 19a. Base of the leaves cuneate and acute, surfaces of the leaves
 concolor; flower-buds about 20 mm long, anther about 14
 mm long 16. **Q. obtusata** Briq.
 b. Base of the leaves obtuse or rounded, surfaces of the leaves
 discolor; flower-buds about 17 mm long, anther about 10
 mm long 10. **Q. verruculosa** Staff.

1. **Qualea rubiginosa** Staff. nov. spec. (fig. 4).

Subgenus *Qualea*, sectio *Trichanthera* Staff. Arbor parva. Ramuli juveniles, petioli et foliorum juvenilium pagina inferior ferrugineo-pubescentes. Glandulae ellipticae, circa 1 mm longae. Petiolus circa 5 mm longus. Lamina rigide coriacea, lanceolato-oblonga vel elongato elliptico-oblonga, circa 7–10 cm longa et $2\frac{1}{2}$ –3 cm lata, apice rotundata, obtusa vel breviter obtuse-acuminata, valde mucronata, basi obtusa vel rotundata; nervis lateralibus ultra 20 per cm; venis numerosissimis. Inflorescentia thyrsoides terminalis, cincinnis 2–3 floris, rachi, bracteis, pedicellis et calyce extra ferrugineo-pubescentibus; bracteis deciduis, triangularibus, circa 1 mm longis, pedicellis 5–10 mm longis. Alabastra 9–11 mm longa, subacuta, gracilia. Calycis laciniae minores

triangulări-ovatae, acuto-acuminatae, laterales circa 2 mm longae, anteriores circa 3 mm longae: lacinia major circa 9-11 mm longa, calcare cylindrico, circa 3-5 mm longo. Petalum glabrum sed margine subciliatum, circa 2 cm longum et $1\frac{1}{2}$ -2 cm latum. Anthera

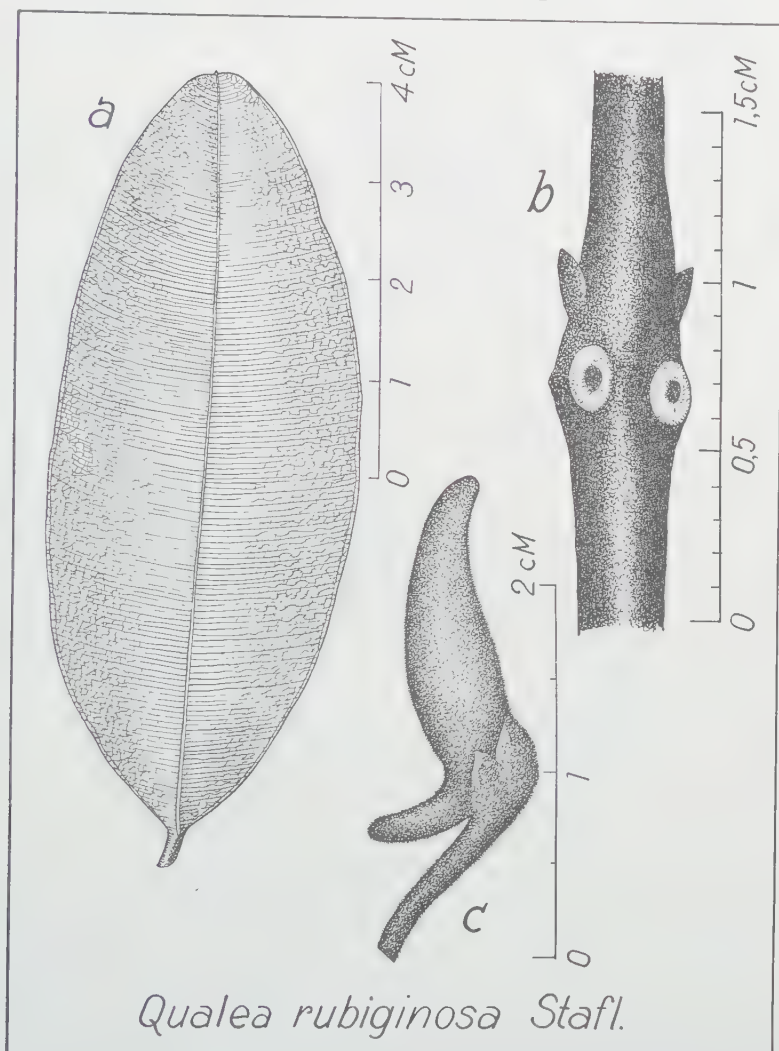


Fig. 4. *Qualea rubiginosa* Stafl. a. Leaf; b. stipular glands; c. flower-bud.

barbata, lineari-oblonga, circa 6-8 mm longa. Filamentum ad 10 mm longum. Staminodia 1-2, linearia, circa 1 mm longa. Ovarium clongato-ovoideum, ferrugineo-hirtum, indumento styli partem $\frac{1}{2}$ - $\frac{1}{3}$ inferiorem occupante.

Holotype: Cardona 1905 in US.

Distribution: Once collected.

VENEZUELA, Guayana: Uaipari R. (affl. of Ikabar), Caroni, Cardona 1905.

Ecology: In savannas (llanos), 500 m, fl. Oct.

Observation: Differs from the other species of this section by the ferrugineous (rubiginose) tomentum on the young parts and by the small flowers and narrow leaves.

2. ***Qualea trichanthera*** Spruce ex Warm. Flora Bras. **13**(2): 35. 1875; Benoist 1915 p. 239, 241.

Large tree. Young branchlets, petioles, midrib of the leaves, inflorescences and outside of the calyx puberulous. Stipular glands suborbicular or elliptic, subprominent, concave. Petioles slender, 9–12 mm long. Leaf-blades somewhat rigid, glabrous except the midrib, elongate-elliptic or suboblong, $7-10 \times 3-4$ cm, the apex acute-acuminate and mucronulate, the base acute in youth, obtuse or rounded in age; the lower side of the midrib provided with two narrow wings; more than 10 thin, strictly parallel lateral nerves per cm; numerous veinlets on the entire surface. Inflorescence composed of terminal and axillary racemes (10–15 cm long) bearing 1–3 flowered cincinni; the pedicels slender, 5–8 mm long; the bracts deciduous, acute, 1–2 mm long. Flower-buds about $11-14 \times 2-3$ mm, the apex acute, the back rounded but with a thin rib near the top. Minor calyx-lobes ovate or deltoid, acute, the anterior ones 2–3 mm long. Spurred lobe about 11–14 mm long, the spur straight or somewhat recurved, constricted near the base, about half as long as the pedicel. Petal white, streaked with red, glabrous except the subpilose lower side of the base. Anther barbate, 7–9 mm long. Ovary lanuginose, elongate-ovoid; the lower half of the style also lanuginose. Capsules unknown.

Holotype: Spruce 2706 in C. Isotypes in: BM, BR, C, F, G, GH, GOET, K, NY, OXF, P, W.

Distribution: Upper Amazonia.

BRAZIL, Amazonas: Near Panuré on R. Uaupès, Spruce 2706; S. Paulo de Olivença, Krukoff 8834; Curucuhy, S. Gabriel, Froes 21443.

Ecology: On terra firma in high forest; fl. Nov.

3. ***Qualea clavata*** Stapf. nov. spec. (fig. 5).

Subgenus *Qualea*, sectio *Trichanthera* Stapf. Arbor magna. Ramuli juveniles subpuberuli, decorticantes, seniores et folia glabra. Glandulae subellipticae, vix prominentes, $\frac{1}{2}$ –1 mm longae. Petiolus robustus, 7–9 mm longus. Lamina rigide coriacea, subnitida, elliptica vel elliptico-oblonga, circa 8–10 cm longa et $3-4\frac{1}{2}$ cm lata, apice mucronulata, breviter acuto-acuminata vel subobtusata, basi obtusa; nervis laterilibus in utraque pagina prominentibus, ultra 20 per cm; venis numerosis. Inflorescentia thyrisoidea, multiflora, terminalis et axillaris; cincinnis 1–2 floris; rachi (ad 12 cm longi) et pedicellis (circa 5 mm longis) ferrugineo-subpuberulis. Flores fragrantis. Alabastra subsericea, subellipsoidea vel subcylindrica, obtusa, circa 14–17 mm longa et 4–5 mm lata. Calycis laciniae minores ciliatae, subovatae, subobtusae, laterales circa 3 mm longae, anteriores circa 4 mm longae; lacinia major oblonga. Calcar clavatum, 8–10 mm longum et 3–4 mm latum, apice rotundatum, basi constrictum. Petalum glabrum sed margine ciliatum,

album macula lutea, suborbiculare. Anthera barbata, circa 12 mm longa, apice acuta, filamentum plusminusve aequans. Staminodia linearia, circa 1 mm longa. Ovarium subsericeum, ovoideum, indumento styli partem $1/6-1/3$ inferiorem occupante. Capsula ignota.

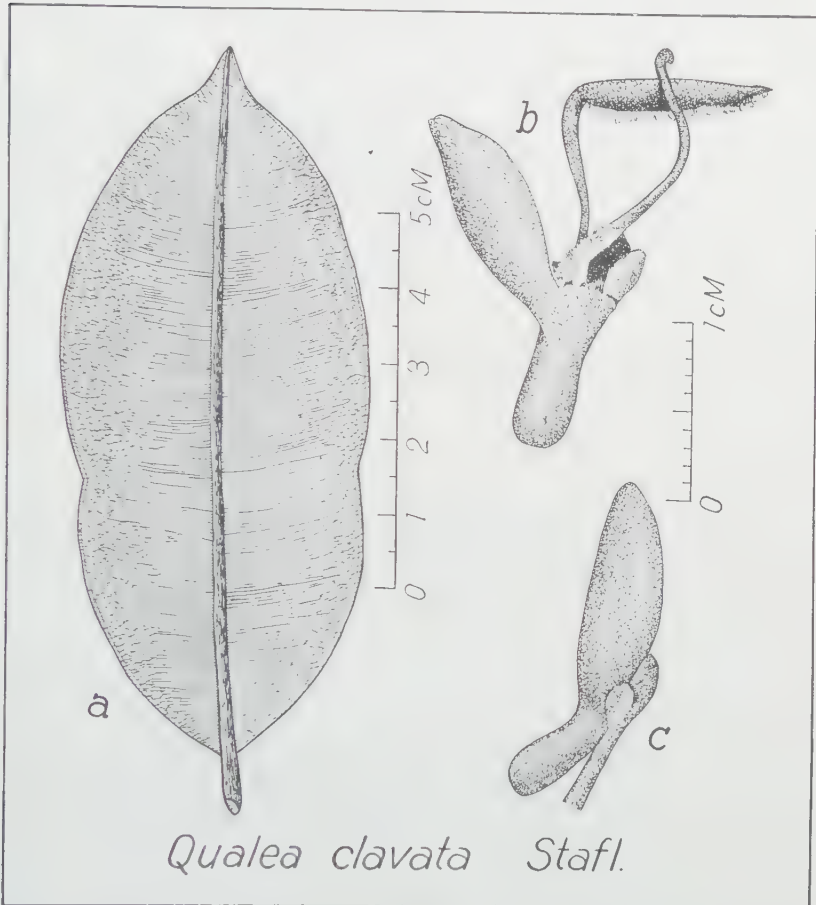


Fig. 5. *Qualea clavata* Stafl. a. Leaf; b. flower (the petal taken away); c. flower-bud.

Holotype: *Ducke* RB 23793 in U. Isotypes in: G, K, S, US.

Distribution: Twice collected.

BRAZIL, Amazonas: Sao Paulo de Olivença, *Ducke* RB 23793; —, — 1061.

Ecology: In woods outside the range of annual floods; fl. Oct.

Observation 1: Characterised by the rigid leaves, the large flowers with the short clavate spur and the indumentum of the style.

Observation 2: The type-specimen was referred to as *Qualea albiflora* by *Ducke* (1938 p. 37).

4. ***Qualea gardneriana*** Warm. *Flora Bras.* **13**(2): 35. *t.* 5. 1875; Benoist 1915 p. 239, 241.

Large tree. Young branchlets, rachis, petioles, and lower side of

the midrib subpuberulous. Young branchlets subterete, the cortex exfoliating (small fragments). Stipular glands subprominent, elliptic or suborbicular, about 1 mm long, the callous margin greyish. Petioles 5–9 mm long. Leaf-blades coriaceous, ovate or ovate-elliptic, $6-7 \times 3\frac{1}{2}-4$ cm, the apex acuminate and mucronate, the base mostly rounded, in younger leaves also acute or obtuse. Midrib winged below. Lateral nerves subconspicuous, scarcely prominent on either side, 15–25 per cm. Veinlets numerous on the entire surface. Flowers in 1–3 flowered cincinni in the axils of the leaves and in terminal racemes, apparently in clusters because of the short pedicels and long spurs. Pedicels pubescent, 3–4 mm long. Flower-buds sub-cylindrical, 13–15 mm long, acute, the back rounded. Outside of the calyx densely — somewhat adpressed — pubescent with mixed longer and shorter hairs; the minor lobes subovate, subacute or obtuse, 2–3 mm long; the spur 4–6 mm long, cylindrical. Petal white painted with red. Anther barbate, obtuse, about 10 mm long. Staminodes linear, about 1 mm long. Ovary elongate-ovoid, like the lower half of the style densely fulvous-hirsute, the latter elongated and coiled. Capsule unknown.

Holotype: *Gardner* 2841 from Piahy in W. Isotypes in: BM, F, G, GH, K, NY, P.

Distribution: Once collected.

BRAZIL, Piahy: *Gardner* 2841 (The Paris and the second Vienna and BM specimens are labelled "Pernambuco", district of Rio Preto).

Ecology: Fl. Sept.

Observation: The Piahy specimen in Vienna bears a label with WARMING's handwriting and agrees completely with his figure (l.c. t. 5).

5. ***Qualea wittrockii*** Malmc. Ark. Bot. Stockholm 5(6): 6. 1905; Ducke 1922 p. 195; — 1938 p. 37. *Qualea arirambae* Ducke 1915 p. 47.

Large tree. Leaves and branchlets glabrous or nearly so; the cortex of the latter exfoliating. Stipular glands elliptic, subprominent, $1\frac{1}{2}-2$ mm long, the callous margin greyish-brownish. Petioles 3–7 mm long. Leaf-blades coriaceous, oblong-lanceolate or subelliptic-oblong, $8-17 \times 3-5$ cm, the apex gradually acute-acuminate, the base mostly distinctly cordate or rounded, sometimes subobtuse, often complicated; the midrib not winged; the lateral nerves very slender, not prominent, 5–10 major ones per cm and several minor ones in between each pair; veinlets numerous. Inflorescence a terminal panicle of up to 10 cm long racemes bearing 1–3 flowered cincinni, sometimes some racemes in the axils of the upper leaves. Pedicels and top of the rachis puberulous, the former 2–4 mm long. Flower-buds acute, up to 13 mm long. Calyx sericeous outside, the minor lobes triangular or ovate, acute, about 2–3 mm long, the spurred lobe provided with a dorsal rib, 12–15 mm long, the spur cylindrical, straight or recurved, up to 5 mm long. Petal white with pink nerves and basically orange central nerve, obovate-orbicular, up to $2\frac{1}{2}-3$ cm long and wide. Anther barbate, 8–10 mm long; the filament up to 7 mm long. Staminodes and rudimentary petals linear, about 1 mm long. Ovary ovoid-conical, like the

lower 2/3 of the style pilose; the latter about 14–18 mm long and often spirally coiled. Capsules about 3×1 cm, verruculose, apically acuminate.

Holotype: *Malme* II 2248 in S. Isotypes in: BM, F, G, US. Holotype of *Q. arirambae* Ducke: *Ducke* PG 14869 in PG, isotypes in: BM, G, K, P, RB, S, U, US.

Distribution: Throughout Brazilian Para and Amazonas, type-collection from Matto Grosso.

BRAZIL, Matto Grosso: Chapada, *Malme* II 2248. Para: Ariramba, *Ducke* RB 5730 = PG 14869; —, — PG 11425; —, — PG 8001; Bella Vista on Rio Tapajoz, *Ducke* PG 16491 = RB 8422; Porto de Moz, lower Xingu, *Ducke* PG 16666; Obidos, *Ducke* PG 15669; Montealegre, *Ducke* PG 16143. Amazonas: Borba, *Ducke* 992; Rio Negro between Camanaos and Sao Gabriel, *Ducke* RB 23487.

Ecology: Found in "cabeceiras": swampy forests of river sources. In Para also in the Igapó (swampy forests along rivers); fl. Sept.–Febr. In Matto Grosso fl. in dry season. Sec. *Malme* (l.c. p. 6) proterandric; often visited by colibris.

Vernacular names: Mandioqueira, Umiri-rana (Para).

Observation: Mentioned by *Ducke* (1905 p. 304) as *Q. aff. acuminata*.

6. ***Qualea retusa*** Spruce ex Warm. *Flora Bras.* **13**(2): 34. *t.* 4 *fig.* 1. 1875; — 1889 p. 22; Glaziou 1905 p. 30; *Ducke* 1915 p. 46; — 1938 p. 37; Benoist 1915 p. 239, 240; Hoehne 1951 p. 257.

Tree of medium size. Young branchlets with subpilose exfoliating cortex (small fragments). Stipular glands elliptic, $\frac{1}{2}$ –1 mm long. Petioles subpilose, 1–5 mm long. Leaf-blades obovate-oblong or subelliptic, $3\text{--}5 \times 2\text{--}3$ cm; the apex rounded or obtuse, mostly distinctly retuse, mucronulate; the base obtuse or rounded; the surfaces somewhat shining, glabrous; the midrib somewhat hairy and narrowly winged below; lateral nerves about 10–20 per cm; veinlets few, mainly near the margin. Flowers fragrant, solitary or in pairs in the axils of the leaves. Pedicels 2–10 mm long. Bracts linear, 2–3 mm long. Flower-buds acuminate, provided with a weak dorsal ridge. Calyx sericeous outside, the minor lobes deltoid, acute, ciliate, the lateral ones about half as long as the about 2–3 mm long anterior ones; the spurred lobe 12–14 mm long, the spur subclavate or cylindrical, straight or recurved, 5–9 mm long. Petal white with a yellow midrib and a few vermilion spots on each side, ovate-suborbicular, up to 4×3 cm. Anther barbate, about 6–8 mm long, the filament up to 10 mm long. Stamines about 1 mm long. Ovary and lower third of the style whitish-yellowish lanuginose, the latter often coiled. Capsules about 2 cm long, the exocarp — in age — releasing from the endocarp, the valves lanceolate-elliptic, apically acute or acuminate. Seeds $10\text{--}12 \times 3\text{--}4$ mm, the winged half included.

Holotype: *Spruce* 1838 in M. Isotypes in: BM, G, GH, K, OXF, P, U, W. Cotypes: *Spruce* 1290 (K, P) and *Riedel* s.n. along Rio Negro (OXF, P). See Obs. 1.

Distribution: Mainly in the eastern parts of Brazilian Amazonas.

BRAZIL, Amazonas: Manaos, *Spruce* 1838; —, — 1290; —, — 1132; —, s.n.; —, *Riedel* s.n.; —, *Ducke* PG 11546 = RB 14060; —, — 1277; —, *Ule* 8883; —, *herb. Schwacke* III 280; —, — III 487; Rio Branco, Caracarahy, *Kuhlmann* 181 = RB 2926; Rio Negro, Preto Campinha, *Froes* 22758, 22759; Rio Madeira, Porto velho, *Ducke* 221 = RB 34660; —, — 227; Maués, *J.M. Pires* 55; Manuas, *Froes* 21616. Para: Lac de Faro, *Ducke* PG 6922. Minas Geraes: Campos de Inficionado, *Glaziou* 13810.

Ecology: On sandy, often marshy, terra firma, also along rivers in forests outside the reach of the seasonal floods. Flowering reports from nearly each month but mainly from April till June (rainy season).

Vernacular names: Umiry-rana (false Umiry or Umiri: *Humiria floribunda* Mart.).

Observation 1: According to manuscript notes in the Copenhagen herbarium Warming used Munich specimens for his analysis and it is highly probable that the Munich specimen of Spruce 1838 is the holotype.

Observation 2: For *Q. retusa* var. *coriacea* Ducke see *Q. obtusata* (no. 16).

7. ***Qualea albiflora*** Warm. Flora Bras. **13**, 2: 36. 1875; Pulle 1906 p. 250; Benoist 1915 p. 241; — 1931 p. 163; Pfeiffer 1926 p. 353; Ducke 1930 p. 145; — 1938 p. 37; Smith 1939 p. 188; Amshoff 1948 p. 9, 17; Menega 1948 p. 44 (anatomy); Stafleu 1948(2) p. 644; — 1951 p. 191; Macbride 1950 p. 876. *Qualea glaberrima* Ducke 1915 p. 46 t. 19F; — 1922 p. 195.

Large or medium-sized tree. Young branchlets and leaves subpuberulous, the older ones glabrous. Branchlets brownish-purplish in youth, greyish in age, the cortex not exfoliating. Stipular glands scarcely prominent, about 1 mm long. Petioles 4–8 mm long. Leaf-blades subcoriaceous, thin, obovate or subelliptic, 4–8 × 2–3½ cm; the apex obtuse or subrotundate or shortly obtuse-acuminate, the base acute or subobtusate; more than 20 lateral nerves per cm; veinlets few. Flowers fragrant, solitary or in 2–3 flowered cincinni, the latter axillary or arranged in racemes, the rachis, the pedicels and the outside of the calyx subpuberulous or nearly glabrous, the pedicels 6–10 mm long. Flower-buds acute or acuminate, 11–14 × 3–4 mm. Minor calyx-lobes acute, ciliate, 1–4 mm long; the spurred lobe 12–16 × 6–8 mm, ciliate; the spur 5–7 × 2–3 mm, slightly recurved or nearly straight, clavate. Petal white with an orange-yellow base, suborbicular, 2–4 cm long and wide, apically truncate or emarginate, glabrous except the subpilose base. Anther barbate, acute-acuminate, about 6–8 mm long; the filament up to 10 mm long. Staminodes and rudimentary petals often present, ½–1 mm long. Ovary sericeous. Style glabrous except the basal 1–2 mm, spirally coiled, 15–20 mm long. Capsules ellipsoid, blackish, rugulose, nitid, subacuminate, about 3 cm long.

Lectotype: *Kappler* 2037 in W. Isotypes in: F, GOET, L, P, U, Holotype of *Q. glaberrima* Ducke: *Ducke* PG 15491 in PG; isotypes: BM, F, G, P, US. See also obs. 1.

Distribution: Guiana, Brazilian Para and Amazonas.

BRAZIL, Para: Belem, *Ducke* PG 15491; —, — PG 17027; —, — PG 15550; Gurapá, *Ducke* PG 16559 = RB 8461; *N.T. da Silva* 88. Amazonas: Manès, *Ducke* RB 23486.

FRENCH GUIANA: Maroni, *Mélinon* 361; —, — 390.

BRITISH GUIANA: Essequibo R., *A. C. Smith* 2709.

SURINAME: Numerous collections, see Stafleu 1951 p. 192; e.g.: Upper Marowijne R. (Maroni), *Kappler* ed. *Hohenacker* 2037.

Ecology: In "terra firma" forests; fl. Sept.–Dec.

Vernacular Names: BRAZIL, Para: Mandioqueira. SURINAME: Kwarie, Gronfoloe; full details see Stafleu 1951 p. 192.

Observation 1: The *Kappler* 2037 specimen from Vienna is the lectotype: Warming mentions the number without reference to a herbarium.

Observation 2: The inner wall of the calyx is often provided with smallish, irregularly placed scales.

8. ***Qualea nitida*** Staffl. nov. spec. (fig. 6).

Subgenus *Qualea*. Arbor. Ramuli juveniles glabri, subteretes, haud decorticantes; gemmis subpuberulis, acutis, circa 1 mm longis. Glandulae ellipticae, circa $\frac{1}{2}$ mm longae, vix prominentes. Petiolus 2–4 mm longus. Lamina glabra, tenuiter subcoriacea, nitida, lanceolato-

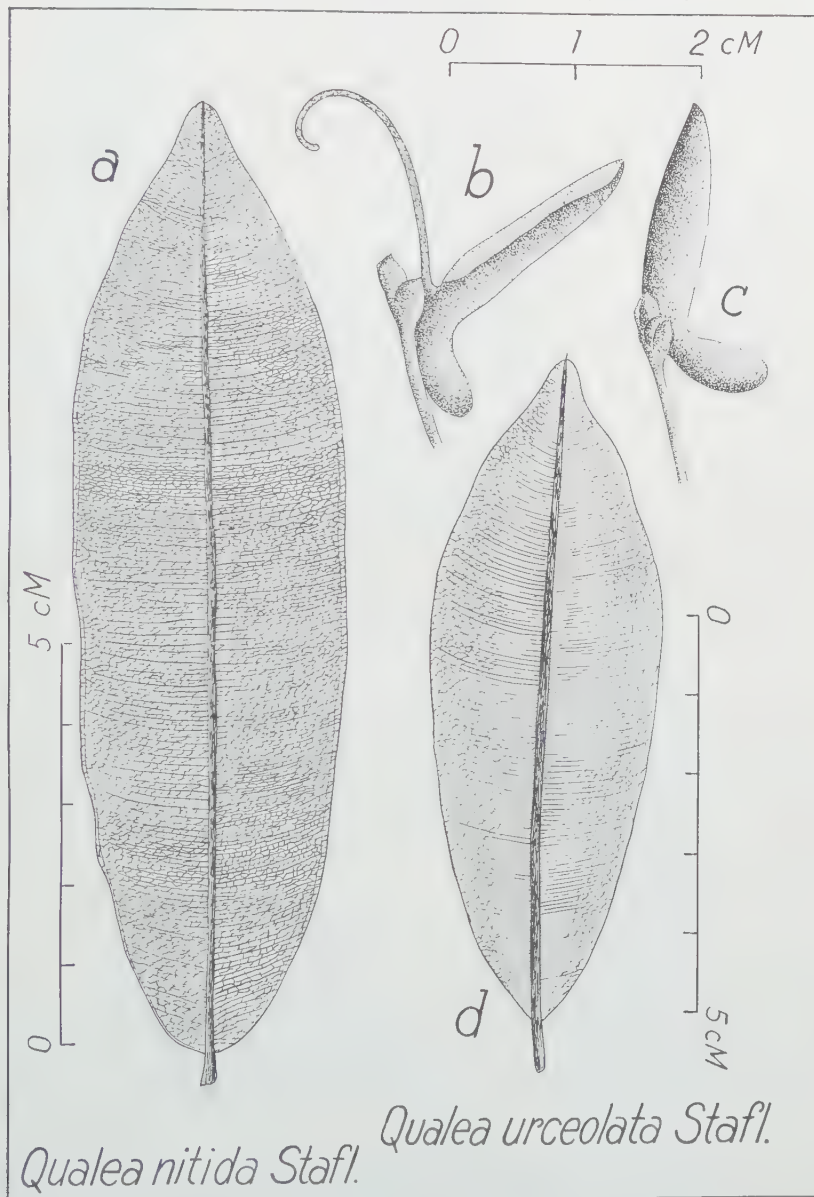


Fig. 6. a. *Qualea nitida* Staffl., leaf. b–d. *Qualea urceolata* Staffl. b. Calyx and style; c. flower-bud; d. leaf.

oblonga, 10–14 cm longa et 3–4 cm lata, in siccis supra virescens, infra fusca; costa bialata, alis ciliatis; nervis lateralibus in utraque pagina subprominentibus, ultra 10 per cm; venis paucis prope marginem; costis marginalibus duabus tenuibus. Flores et fructus ignoti.

Holotype: *Tate* 915 in US (ster).

Distribution: Once collected.

VENEZUELA, Aguita, slopes of Mount Duida, *Tate* 915.

Ecology: 1300 m.; fl. Jan.

Observation: The section to which the species belongs cannot be established with any certainty as long as the flowers remain unknown.

9. *Qualea rigida* Stapf. nov. spec. (fig. 7).

Subgenus *Qualea*, sectio *Trichanthera* Stapf. Arbor. Ramuli glabri, cortice nigro in squamulas minutas soluto. Glandulae subellipticae, circa 2 mm longae, vix prominentes. Petiolus crassus, 3–7 mm longus, basi incrassatus. Lamina rigide coriacea, glabra, lanceolata vel lanceolato-elliptica, 8–10 cm longa et 2 $\frac{3}{4}$ –4 cm lata, supra subnitida, subtus opaca, apice mucronata, obtusa vel acuta, raro rotundata et subretusa, basi cordata vel subrotundata; nervis lateralibus ultra 10 per cm, leviter curvatis; venis paucis prope marginem; costis marginalibus duabus, tenuibus. Inflorescentia thyrsoides, terminalis, densiflora, in typo circa 7 cm longa; cincinnis 2–3 floris; pedicellis, bracteis et calyce extra ferrugineo-pubescentibus; bracteis triangularibus, acutis, circa 2 mm longis; pedicellis 4–10 mm longis. Flores fragrantis. Alabastra elongato-conica, circa 20 mm longa, apice acuta, recurvata. Calycis laciniarum minores triangulares, acutae, 3–5 mm longae, lacinia major suboblonga. Calcar cylindricum, 3–5 mm longum et 1–2 mm latum. Petalum album, versus basim lineis luteis et rubris notatum, apice subrotundatum. Petalum secundum rudimentarium ellipticum, acuminatum, circa 2–3 mm longum. Anthera barbata, acuta, circa 10 mm longa; filamentum circa 13–15 mm longum. Staminodia linearia, circa 1 mm longa. Indumentum styli partem 1/5–1/3 inferiorem occupans. Capsula ignota.

Holotype: *Cardona* 1762 in US

Distribution: Venezuelan-Guianan Mountains.

VENEZUELA, Guayana: Orillas del Caroni, *Cardona* 1762.

BRITISH GUIANA, Upper Cujang R., *Ri. Schomburgk* 1537; Annaway Valley, *Ro. Schomburgk* 19.

Ecology: Type specimen fl. Oct., 720 m.; *Schomburgk* specimina from savannas.

Observation 1: The specimen *Schomburgk* 1537 was preserved in Berlin; the present author saw a photograph. It is possible that this specimen was the type of *Qualea muelleriana* Schomburgk (nomen nudum) but the label does not exactly correspond with the details given by Schomburgk (1848 p. 1099). Therefore the name *Qualea muelleriana* cannot be maintained: Schomburgk neither described nor typified such a taxon.

Observation 2: The nearly allied *Q. nitida* has much thinner leaves which are acuminate and provided with a winged midrib; its stipular glands are much smaller; *Q. esmeralda* differs from *Q. rigida* by the apically and basically rounded elliptic leaves which are twice (not thrice) as long as wide, by the obtuse straight flowerbuds and the smaller stipular glands.

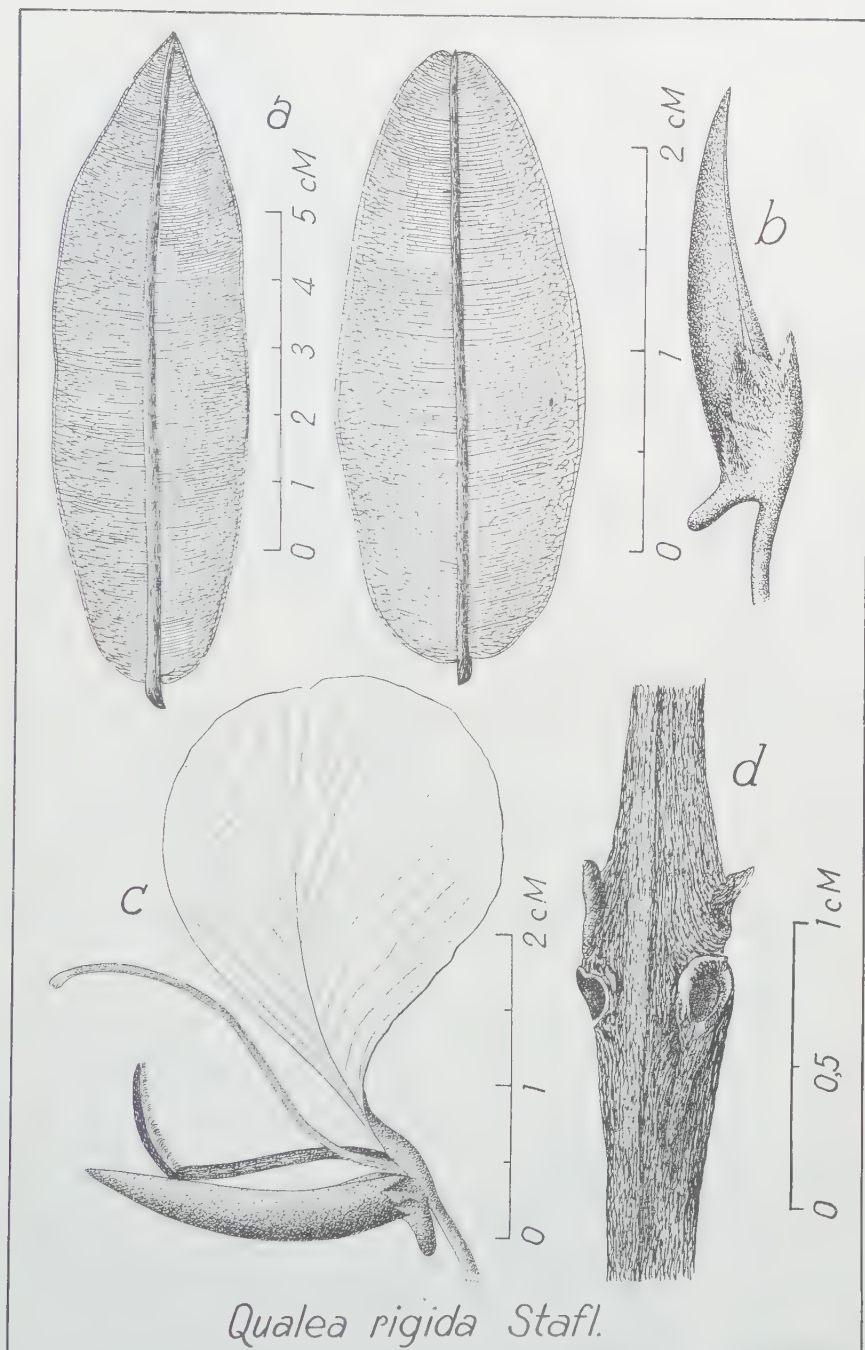


Fig. 7. *Qualea rigida* Stafl. a. Leaves; b. flower-bud; c. flower; d. stipular glands.

10. ***Qualea verruculosa*** Staf. nov. spec. (fig. 8).

Subgenus *Qualea*, sectio *Trichanthera* Staf. Arbor parva. Ramuli glabri haud decorticantes. Glandulae ellipticae, circa 1 mm longae, haud prominentes. Petiolus 5–9 mm longus, basi incrassatus. Lamina subrigide coriacea, glabra, oblonga, subelliptica vel subovata, 5–6 cm longa et $2\frac{1}{2}$ –4 cm lata, apice rotundata vel rotundato-obtusa, saepe emarginata vel retusa, basi obtusa vel subrotundata; costa subtus bialata; nervis lateralibus in utraque pagina subprominentibus, ultra 10 per cm; venis numerosis. Cincinni 1–2 flori in racemos axillares et terminales paucifloros dispositi. Pedicelli subpuberuli, 4–8 mm longi. Alabastra fulvo-subpuberula, cylindrica, obtusa, circa 17 mm longa et 3 mm lata. Calycis laciniae minores ovatae, acutae, ciliatae, laterales circa 2 mm, anteriores circa 3–4 mm longae; lacinia major oblonga, circa 17 mm longa. Calcar subclavatum basi constrictum, 4–6 mm longum. Petalum glabrum sed margine ciliatum, $2\frac{1}{2}$ –3 cm longum et latum; colore ignoto. Petala rudimentaria 1–2, linearia, circa 1–2 mm longa. Anthera barbata, apice acuta, basi obtusa, circa 10 mm longa; filamentum 10–14 mm longum. Staminodia 1–2, circa 1 mm longa. Ovarium ovoideum. Stylus circa 20 mm longus post anthesim curvatus, indumento styli partem $1/8$ – $1/10$ inferiorem occupante. Capsula (immatura) ellipsoideo-obovoidea, valvis nigris minute verruculosis.

Holotype: *E. G. Holt* ♂ *E. R. Blake* 717 in US.

Distribution: Upper Amazonia.

VENEZUELA, Amazonas: Cerro Yapacana, upper Rio Orinoco, *E. G. Holt* ♂ *E. R. Blake* 717.

BRAZIL, Amazonas: Rio Curicuriary, affl. Rio Negro, *Ducke* RB 34668.

Ecology: Type specimen fl. et fr. April; *Ducke* specimen fl. Nov.

Observation: This species differs from *Q. obtusata* by the shape of the leaves, the size of the flower-bud and the length of the anther. *Q. esmeraldae* has larger leaves, inflorescence and flowers, longer petioles and an entirely glabrous petal.

11. ***Qualea esmeraldae*** Standl. Bull. Torr. Bot. Club **58**: 380. 1931.

Shrub or small tree. Branchlets and leaves glabrous. Cortex somewhat exfoliating. Stipular glands subprominent, blackish, about 1 mm long. Petioles 4–14 mm long. Leaf-blades oblong or elliptic-oblong, 7 – 10×3 – $5\frac{1}{2}$ cm, reddish-brown below; the apex rounded and often retuse, sometimes subobtuse or mucronate; the base rounded; the nervation subprominent on both sides; 10–20 lateral nerves per cm; veinlets numerous. Inflorescence a terminal raceme composed of 1–2 flowered cincinni. Rachis brownish puberulous. Pedicels subpilose, firm, 4–7 mm long. Flower-buds brownish-puberulous, straight, subacute, 16–22 mm long. Minor calyx-lobes acute, ciliate, the lateral ones about 2 mm long, the anterior ones about 4 mm long; the spurred lobe elliptic, up to 22 mm long, the back provided with a rib; the spur stretched along the pedicel, cylindrical, 3–5 mm long, not or only slightly constricted near the base. Petal pink or turning white, suborbicular or subelliptic, about 3 – $3\frac{1}{2}$ cm long. Rudimentary petals

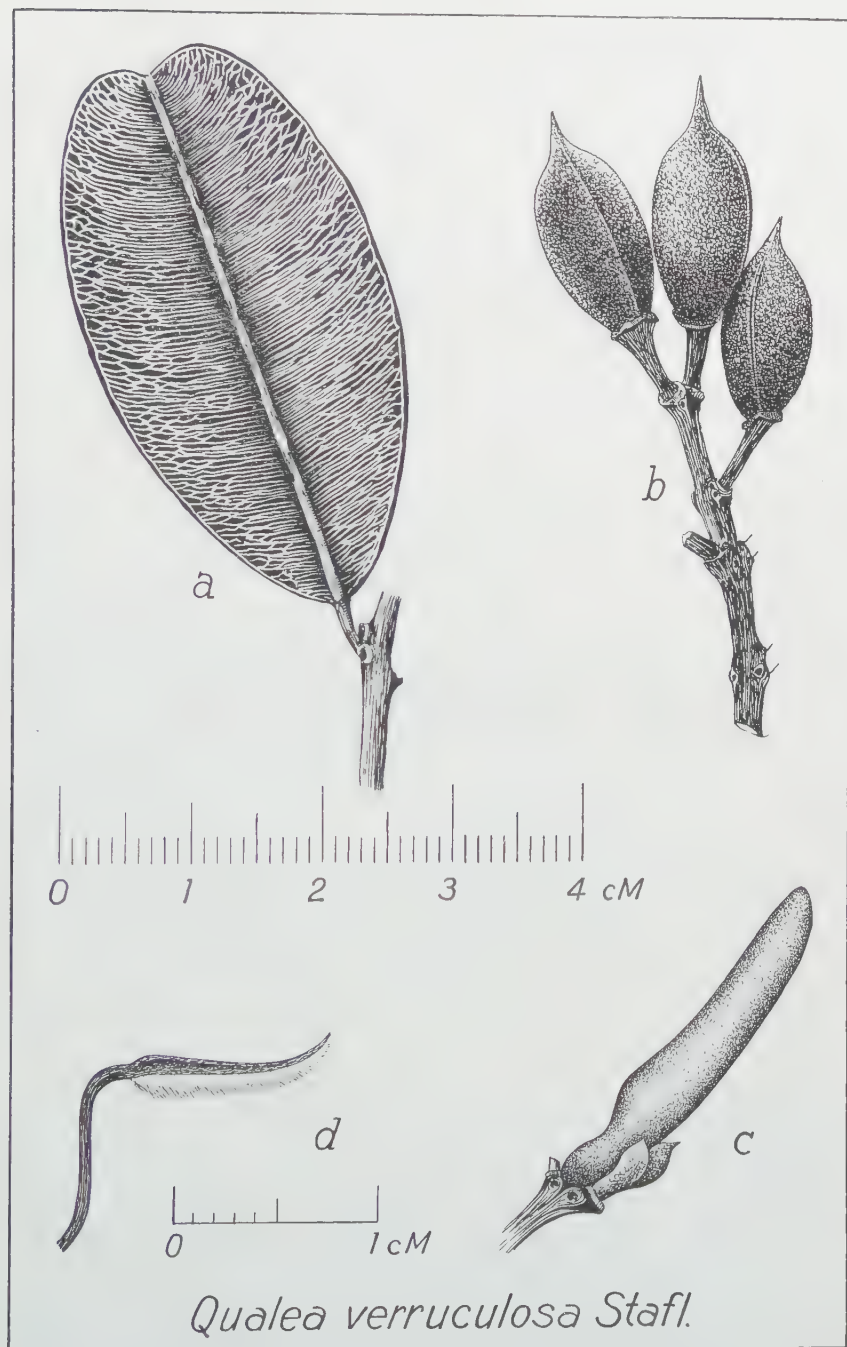


Fig. 8. *Qualea verruculosa* Staf. a. Leaf; b. fruits; c. flower-bud; d. stamen.

linear, about 1–2 mm long. Anther barbate, about 10 mm long, the filament in anthesis up to 2 cm long. Staminodes flask-shaped, about 1 mm long. Ovary pyramidal, ferruginous-hirsute; the style up to $2\frac{1}{2}$ cm long, often coiled, the basal 1–3 mm hirsute. Capsules ellipsoid, glabrous, verruculose, acute acuminate on account of the persistent base of the style.

Holotype: *Tate* 194 in NY.

Distribution: Southern Venezuela.

VENEZUELA, Amazonas: Esmeralda, *Tate* 194; —, *Steiermark* 57828; Rio Orinoco, San Antonio, *Ll. Williams* 15063.

Ecology: In savannas, about 100 m.; fl. Aug.–Oct.; fr. Oct.–Apr.

Observation: See observation under no. 10: *Q. verruculosa*.

12. ***Qualea cassiquiarensis*** Spruce ex Warm. *Flora Bras.* **13**(2): 34. 1875; Ducke 1933 p. 43.

Large or medium-sized tree. Branchlets and leaves glabrous. Cortex blackish, not exfoliating. Stipular glands not prominent, $\frac{1}{2}$ –1 mm long. Petioles firm, 1– $2\frac{1}{2}$ cm long and 2–3 mm wide. Leaf-blades rigidly coriaceous, oblanceolate, subelliptic or suboblong, 10–17 \times 4–6 cm; the apex obtuse and mucronulate; the base obtuse; the midrib narrowly winged below, the wings ciliate; 15–25 lateral nerves per cm, subprominent on both sides; veinlets mainly near the margin. Inflorescence a terminal panicle composed of 1–2 flowered cincinni, puberulous, about 10 cm long. Pedicels firm, 5–9 mm long. Flower-buds brownish-puberulous, conical, the back rounded, the apex obtuse, about 20 mm long and 5–6 mm wide near the base. Flowers fragrant. Minor calyx-lobes subequal, 3–6 mm long. Spur stretched along the pedicel, wide, almost bursiform, not or scarcely constricted near the base and situated almost in the produced part of the back of the lobe, 3–4 \times 2–4 mm. Petal white with a yellow spot, obcordate, up to 4 cm long. Rudimentary petals not present. Anther barbate, about 15 mm long; the filament glabrous, up to 10 mm long. Staminodes absent(?). Ovary ovoid, fulvous-lanuginose (the hairs about 2 mm long), more or less abruptly merging into the style; the latter glabrous except the basal 1 mm, often elongated and coiled, about $2\frac{1}{2}$ cm long. Capsules unknown.

Holotype: *Spruce* 3298 in C. Isotypes in: BM, BR, F, G, GH, GOET, K, NY, OXF, P, W; B (vide photograph in F).

Distribution: Brazilian and Venezuelan Amazonas.

BRAZIL, Amazonas: Cassiquiare, Vasiva and Pacimoni R., *Spruce* 3289; Manaos, *Ducke* RB 23489; —, — 61; —, — 46.

VENEZUELA, Amazonas: San Carlos, Rio Negro, *Ll. Williams* 14636.

Ecology: In lowland swamp-forests, not reached by seasonal floods ("Igapó"). Flowering reports from March, June, Oct., Nov.

Observation 1: *Q. cassiquiarensis* var. *belemnensis* Ducke (1915 p. 47, 1922 p. 195) is raised to the rank of species: no. 13 *Q. belemnensis*.

Observation 2: The note by Ducke (1938 p. 37) refers to *Q. cassiquiarensis* as well as to *Q. belemnensis* and *Q. urceolata*.

Observation 3: The species is closely allied to no. 13 *Q. belemnensis* and to no. 15 *Q. urceolata*; see observations under those species.

13. **Qualea belemnensis** Staff. nov. spec. (fig. 9).

Qualea cassiquiarensis Spruce ex Warm. var. *belemnensis* Ducke 1915 p. 47; — 1922 p. 195.

Arbor magna. Ramuli juveniles, petioli, gemmae et costa subtus fusco-puberuli. Ramuli juveniles quadranguli et ad apices internodiorum valde compressi, demum subteretes, glabri, haud decorticantes, gemmis parvis, perulis duabus exteriores subcarnosis, glabris. Glandulae $1\frac{1}{2}$ – $2\frac{1}{2}$ mm longae, margine crasso discolore. Petiolus 3–8 mm longus. Lamina coriacea, elliptico-obovata, 10–13 cm longa et $4\frac{1}{2}$ –6 mm lata, apice rotundata et retusa, basi obtusa; costa subtus bialata; nervis lateralibus ultra 15 per cm; venis numerosis. Inflorescentia ferrugineo-pubescent, thyrsioidea, terminalis et axillaris, ad 15 cm longa; cincinnis circa 2 floris; pedicellis 6–10 mm longis. Alabastra ferrugineo-pubescentia, elongato-conica, obtusa, circa 16–18 mm longa et 4–6 mm lata. Calycis laciniae minores ovatae, subacutae vel obtusae, 3–4 mm longae; lacinia major elliptica, rotundata, circa 10 mm lata. Calcar clavatum, 4–7 mm longum et 3–4 mm latum, apice rotundatum, basi constrictum, sub angulo obtuso (120 – 150°) ex alabastro emergens. Petalum glabrum, album macula lutea, subellipticum, carinatum, apice rotundatum, circa 3–4 cm longum. Petala rudimentaria linearia, 1 – $1\frac{1}{2}$ mm longa. Anthera barbata, subacuta, circa 13 mm longa; filamentum circa 15 mm longum. Staminodia linearia, ad 1 mm longa. Ovarium ovoideo-conicum. Stylus post anthesim ad $2\frac{1}{2}$ cm longus, basi pilosus. Capsula 2– $2\frac{1}{2}$ cm longa, acuminata, verruculosa.

Holotype: *Ducke* PG 9610 in US. Isotypes in: BM, G, P.

Distribution: Brazilian Para.

BRAZIL, Para: Belem, *Ducke* PG 9610; —, — PG 15509; Gurupá, *Ducke* PG 15975 = RB 8455.

Ecology: In humid forests, often in marshy places not reached by seasonal floods; fl. Sept.–Jan.: in the middle of the dry season.

Observation: The species differs from *Q. cassiquiarensis* by the clavate spur, the wider leaves, the shorter petioles, the hirsute style which merges gradually into the ovary, etc. It differs from *Q. urceolata* for instance by the rigid leaves, the densely pubescent and obtuse flower-buds.

14. **Qualea ferruginea** Steyermark, Fieldiana Botany **28**: 295. 1952.

Large or medium-sized tree. Young parts ferrugineous-pubescent; branchlets and leaves further glabrous. Stipular glands about 1 mm long. Petioles 3–9 mm long. Leaf-blades coriaceous, elliptic-subobovate or elliptic, 4 – 9×2 – $4\frac{1}{2}$ cm, deepgreen and shining above, yellow or pale green below; the apex mucronulate, rounded or obtuse; the base cuneate or obtuse; the midrib winged below, the wings pubescent; more than 25 lateral nerves per cm; veinlets numerous. Inflorescences terminal, the basal cincinni in the axils of the upper leaves; the cincinni 1–2 flowered; the pedicels densely ferrugineous-pubescent, 4–8 mm long. Flowers fragrant. Calyx ferrugineous pubescent, the minor lobes subequal, acute, 3–4 mm long; the spurred lobe about 15 mm long, suboblong, obtuse or rounded; the spur cylindrical, 3 – 5×1 –2

mm. Petal glabrous, white with orange centre bordered on either side by salmon orange or brick streaks, suborbicular, diameter about 25 mm; rudimentary petals linear, $1-2\frac{1}{2}$ mm long. Anther barbate, $5-6\frac{1}{2}$ mm long; the filament up to 11 mm long. Ovary and lower $\frac{2}{3}$

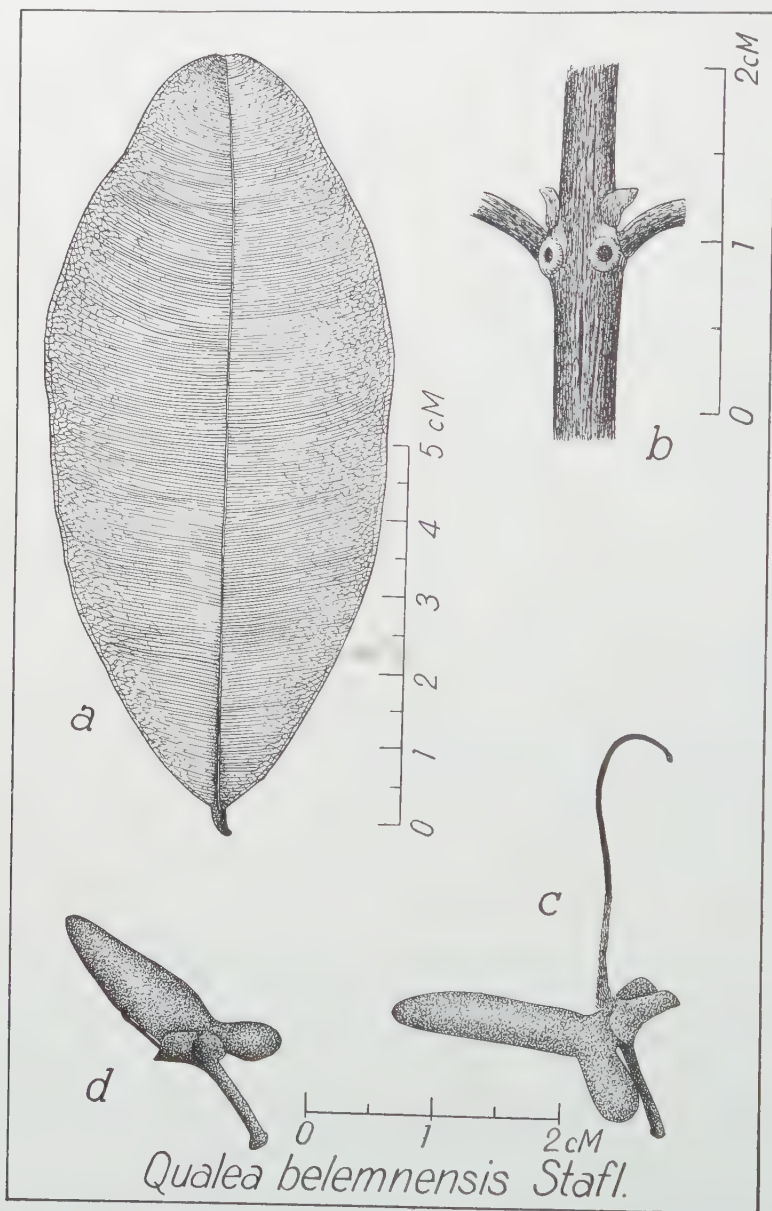


Fig. 9. *Qualea belemnensis* Stafl. a. Leaf b. stipular glands; c. calyx and style; d. flower-bud.

of the style densely ferrugineous-hirtous, the latter coiled, $1\frac{1}{2}$ –2 cm long. Capsules about 3 cm long, verruculose, ellipsoid, the apex acuminate owing to the persistent style-base; the base obtuse.

Holotype: *Steyermark* 60914 in F.

Distribution: Venezuela, Bolivar and adjacent British Guiana.

VENEZUELA, Bolivar: St. Teresita de Kavanayén, *Steyermark* 60914, 60438; Ptari-tepuí, *Steyermark* 60028; between Ptari-tepuí and Sororopan-tepuí, *Steyermark* 60291; Kavanayén, *Lasser* 1759.

BRITISH GUIANA: Upper Mazaruni R., *Pinkus* 240.

Ecology: In forests between 1000 and 1700 m; often along ravines. Fl. Nov.–Dec. Fr. May.

Vernacular names: VENEZUELA, Bolivar: Amu-rieu-wai-yek, keu-pau-rik-orai-yek, minchorai-yek, copai-yek.

15. *Qualea urceolata* Stafl. nov. spec. (fig. 6).

Subgenus *Qualea*, sectio *Trichanthera* Stafl. Arbor magna. Ramuli subteretes, cortice in squamulas parvas fisso. Glandulae ellipticae, circa 1 mm longae, subprominentes. Petiolus 6–10 mm longus. Lamina subcoriacea, glabra, lanceolato-oblonga vel sublanceolato-subelliptica, 8–11 cm longa et 3–4 $\frac{1}{2}$ cm lata, apice mucronulata et breviter obtuso-acuminata, basi obtusa vel subacuta; nervis lateralibus ultra 10 per cm; venis paucis prope marginem. Inflorescentia thyrsoides, racemis elongatis paucifloris usque ad 25 cm longis; cincinnis 1–2 floris; rhachi quadrangulati subpuberuli; bracteis subovatis, acutis, 1–2 mm longis; pedicellis usque ad 12 mm longis, primum subpuberulis. Alabastra elongato-conica, 18–22 mm longa et 4–5 mm lata, apice oblique acuto-acuminata. Calycis lacinae subpuberulae, minores obtusae vel subacutae, laterales circa 2, anteriores circa 3–4 mm longae; lacinia major oblonga. Calcar clavatum, inflatum (urceolatum), 7–10 mm longum et 4–5 mm latum, basi constrictum, apice rotundatum, sub angulo obtuso (120–150°) ex alabastro emergens. Petalum glabrum, album macula lutea, ellipticum, apice rotundatum, 4–4 $\frac{1}{2}$ cm longum et 3–3 $\frac{1}{2}$ cm latum. Anthera barbata, acuta, circa 12 mm longa; filamentum ad 15 mm longum. Staminodia linearia, 1–2 mm longa. Ovarium ovoideum. Stylus ad 2 $\frac{1}{2}$ –3 cm longus, indumento partem 1/3–1/2 inferiorem occupante. Capsula ignota.

Holotype: *Ducke* RB 17742 in U. Isotypes in: K, S.

Distribution: Once collected.

BRAZIL, Para: Belem, *Ducke* RB 17742.

Ecology: In humid forests not reached by seasonal floods; fl. Dec.

Observation 1: Named after the urceolar spur.

Observation 2: Distributed by *Ducke* under "*Q. cassiquiarensis*". It differs from this species by the slender, thin, acute-acuminate leaves, the slender flower-bud, the entirely different spur, etc. It differs from *Q. belemnensis* by the shape and texture of the leaves, the indumentum of the calyx and the acute-acuminate flower-bud.

16. *Qualea obtusata* Briq. Annu. cons. Jard. Bot. Genève **20**: 383. 1919. *Qualea retusa* Spruce ex Warm. var. *coriacea* *Ducke* 1938 p. 37.

Small or medium-sized tree. Branchlets and leaves glabrous, the cortex of the former exfoliating in age. Stipular glands subprominent,

about 1 mm long. Petioles about 5 mm long. Leaf-blades generally obovate, $6-7 \times 2\frac{1}{2}-3\frac{1}{2}$ cm, the apex rounded and often retuse or emarginate, the base cuneate, gradually narrowing towards the petiole; the midrib winged below, the wings ciliate; 10-20 lateral nerves per cm, subprominent; veins numerous on the entire surface. Inflorescence terminal, few-flowered, consisting of 2-4 pairs of opposite flowers (1-flowered cincinni); the pedicels nearly glabrous, 5-7 mm long. Flower-buds about 20 mm long. Calyx subpuberulous or nearly glabrous, the smaller lobes ciliate, obtuse or rounded, the lateral ones about 2-3, the anterior ones about 4 mm long; the spurred lobe about 20 mm long; the spur cylindrical or subclavate, rounded, 5-7 mm long. Petal white with a yellow spot, rounded, about $3-3\frac{1}{2}$ cm long and 3 cm wide. Anther barbate, acute, about 14 mm long; the filament firm, about 15 mm long. Staminodes — if present — linear, about 1 mm long. Ovary fulvous sericeous. Style about $2\frac{1}{2}$ cm long, glabrous except the lower 2-6 mm. Capsules about 3×1 cm, acute-acuminate (owing to the persistent base of the style); the surface black, minutely rugulose.

Holotype: *Spruce* 3341 in G. Isotypes in: BM, BR, C, F, GH, GOET, K, NY, OXF, P, W. Holotype of *Q. retusa* var. *coriacea* Ducke: *Ducke* RB 34669 in RB; isotypes: G, K, P, S, U, US.

Distribution: Amazonia.

BRAZIL, Amazonas: "Ad flumina Cassiquiari, Vasiva et Pacimoni", *Spruce* 3341; Rio Negro, Igarapè Macacuny, *Ducke* RB 34669.

VENEZUELA, Amazonas: Alto Cassiquiare, *Ll. Williams* 15728.

Ecology: In riverine forests inundated by seasonal floods; fl. Sept.; fr. Jan. and May (one report each).

Observation 1: Mentioned by Warming 1875 p. 55 under "*Qualea e serie Calophylloidearum*".

Observation 2: Briquet could not put the species in its proper place for lack of flowers but it is now clear that it belongs to the section *Trichanthera* in the neighbourhood of *Q. ferruginea* and *Q. discolor*. It is characterized by the cuneate leaf-base, the concolorous leaves, the indumentum of calyx and ovary and the minutely rugulose surface of the fruit.

Section B. *Qualea*

Series I. *Calophylloideae* Warm. 1875 p. 30 p.p.

Arbores vel frutices. Folia glabra vel fere glabra, basi haud obliqua; nervis lateralibus numerosissimis (5-50 per cm), creberrimis, rectis, parallelis, sub angulo circo 80° a media ortis, nervo limballi margini parallelo et proximo ($\frac{1}{2}$ -1 mm) junctis. Alabastra subovoidea vel late conica. Calycis lacinia quarta ceteras haud adpressas aequans vel paullo superans (ad $2\frac{1}{2} \times$). Petala rudimentaria et (vel) staminodia saepe adsunt, glabra, parva. Anthera dorsifixa, glabra vel pilosa sed haud unilateraliter barbata, filamentum saepe brevior. Ovarium valde abrupte in stylum transiens, stigmatum capitato vel subcapitato.

Type-species: *Qualea rosea* Aubl. (type-species of genus).

Distribution: Mainly Hylaeian species. The area is disjunct because of the presence of three species in Rio de Janeiro and Minas Geraes.

Key to the species

- 1a. Pedicels $1\frac{1}{2}$ –2 times longer than the flower-buds 2
- b. Pedicels about as long as or shorter than the flower-buds 3
- 2a. Minor calyx-lobes subequal, 10–13 mm long, covering the spur; pedicels firm 17. **Q. themistoclesii** Ducke
- b. Minor calyx-lobes unequal, the lateral ones 5–7 mm long; the spur in anthesis exserted; the pedicels very slender, less than 1 mm wide 18. **Q. pulcherrima** Spruce ex Warm.
- 3a. Flower-buds less than 11 mm long 4
- b. Flower-buds 12–30 mm long. 8
- 4a. More than 10 lateral nerves per cm. Spur shorter than the bud 5
- b. 3–8 major lateral nerves per cm. Spur about as long as the bud see section C. *Costatifolium* p. 192.
- 5a. Minor calyx-lobes subequal. No (rarely only small) extrafloral nectaries near the stipules or the stipular glands 6
- b. Minor calyx-lobes unequal. Conical, 2–3 mm high, extrafloral nectaries near the stipules. Flower-bud 9–13 mm long. 19. **Q. gestasiana** St. Hil.
- 6a. Anther about 2 mm long. Spur exserted in anthesis 7
- b. Anther about 4–5 mm long. Spur hidden by the outer calyx-lobes, even in anthesis. 20. **Q. homosepala** Ducke
- 7a. Stipular ridge present. Leaves long acuminate (1–1½ cm). Flower-buds 8–10 mm long. Filament pilose. 21. **Q. sprucei** Warm.
- b. Stipular ridge absent. Leaves acute or shortly acuminate (less than 5 mm). Flower-buds 5–7 mm long. Filament glabrous 22. **Q. coerulea** Aubl.
- 8a. Ovary gradually merging into the style 9
- b. Ovary more or less abruptly merging into the style 11
- 9a. Stipules of opposite leaves not connected by a distinct elevated stipular ridge 10
- b. Stipular ridge present. 23. **Q. impexa** Macbr.
- 10a. Leaves long acute-acuminate. Spur exserted in anthesis 24. **Q. acuminata** Spruce ex Warm.
- b. Leaves obtuse or somewhat rounded. Spur — in anthesis — hidden by the calyx-lobes. 25. **Q. elegans** Taub. ex Benoist
- 11a. Stipules of opposite leaves connected by a distinct straight or V-shaped stipular ridge 12
- b. Stipular ridge absent 18
- 12a. Spur present 13
- b. Fourth calyx-lobe bag-shaped at the base, no distinct spur 26. **Q. calantha** Pilger
- 13a. Stipular ridge V-shaped 14
- b. Stipular ridge straight 15
- 14a. Petal blue, striped with yellow. Apex of the leaves obtuse or shortly obtuse-acuminate 27. **Q. ingens** Warm. var. **duckei** Staffl.

- b. Petal white with red and yellow. Apex of the leaves long-acuminate 28. **Q. amoena** Ducke
 15a. Leaf-bases rounded or obtuse 16
 b. Leaf-bases cordate 27. **Q. ingens** Warm. var. **ingens**
 16a. Cortex of the branchlets not exfoliating. Petal mainly pink 17
 b. Cortex of the branchlets exfoliating. Petal mainly yellow 29. **Q. rosea** Aubl.
 17a. Anther glabrous or nearly so, apically obtuse, about 8 mm long 30. **Q. lineata** Staffl.
 b. Anther pilose, apically acute, 4-5 mm long 31. **Q. polychroma** Staffl.
 18a. Anther and filament both distinctly pilose 19
 b. Anther, filament or both glabrous or nearly so 20
 19a. Pedicels 7-14 mm long. Spur exerted in anthesis 32. **Q. macropetala** Warm.
 b. Pedicels 4-5 mm long. Spur covered by the calyx-lobes during anthesis 33. **Q. brevipedicellata** Staffl.
 20a. Main colour of the petal white, mostly with a yellow base and painted with red or orange on either side. 21
 b. Main colour of the petal blue, pink or yellow 29
 21a. Leaf-blades 3-5 cm long 22
 b. Leaf-blades 7-15 cm long 23
 22a. Extrafloral nectaries in the axils of the stipules, 2-3 mm high. Anther glabrous. 19. **Q. gestasiana** St. Hil.
 b. No axillary extrafloral nectaries; the base of the stipules subglandular. Anther pilose 34. **Q. tricolor** Benoist
 23a. Apex of the anther two-lobed or emarginate 24
 b. Apex of the anther acuminate, acute or obtuse 25
 24a. Leaf-blades distinctly puberulous 35. **Q. gracilior** Pilger
 b. Leaf-blades glabrous 36. **Q. paraensis** Ducke
 25a. Anther glabrous or with a few hairs 26
 b. Anther pilose on the back 37. **Q. calophylla** Pittier
 26a. Leaves apically acute, obtuse or shortly acuminate 27
 b. Leaves apically long-acuminate (about 1 cm) 28. **Q. amoena** Ducke
 27a. Leaves wider than 3 cm, 2-3 times longer than wide 28
 b. Leaves $1\frac{1}{2}$ - $2\frac{1}{2}$ cm wide, 3-4 times longer than wide 38. **Q. magna** Kuhlmann
 28a. Spur not hidden by the calyx-lobes in anthesis. Flower-bud 17-25 mm long 39. **Q. schomburgkiana** Warm.
 b. Spur hidden by the second calyx-lobe in anthesis. Flower-bud 14-18 mm long 40. **Q. tuberculata** Staffl.
 29a. Petal blue with a yellow base. Cortex of the branchlets not exfoliating 30
 b. Petal mainly pinkish. Cortex of the branchlets exfoliating 41. **Q. decorticans** Ducke
 30a. Leaves lanceolate or suboblong, $2\frac{1}{2}$ - $3\frac{1}{2}$ cm wide. Anther glabrous 42. **Q. suprema** Ducke
 b. Leaves elliptic-oblong, $4\frac{1}{2}$ -6 cm wide. Anther pilose 43. **Q. cyanea** Ducke

17. **Qualea themistoclesii** Ducke, Arch. Inst. Biol. Veg. **4**(1): 38. 1938.

Tree of medium size. Branchlets and leaves glabrous, the cortex of the former not exfoliating. Stipular glands subprominent, diameter about 1 mm, sometimes two per stipule. Petioles firm, 8–13 mm long. Leaf-blades rigidly coriaceous, yellow-greenish above, elliptic or elliptic-oblong, $8-12 \times 4-6$ cm; the apex shortly obtuse-acuminate or -apiculate, sometimes slightly folded; the base rounded or rounded-obtuse; the midrib winged below; the lateral nerves inconspicuous, very slender, about 20–30 per cm; veinlets numerous. Inflorescence an up to 25 cm long raceme of 2–3 flowered cincinni; the pedicels subpuberulous, firm, $1\frac{1}{2}-2$ cm long and $1-1\frac{1}{2}$ mm wide. Flower-buds ovoid, apically somewhat rounded, $10-13 \times 7-9$ mm. Calyx reddish-brown with a greyish subsericeous indumentum, the minor lobes rounded, about 10–13 mm long, the spurred lobe up to 16 mm long, the spur hidden by the outer lobes, up to 10×5 mm. Petal white, up to $3\frac{1}{2}$ cm long and 4 cm wide, obcordate, emarginate. Anther subpilose on the back, about 4 mm long, the base cordate, the apex apiculate; the filament subpilose, firm, up to 13 mm long. Staminodes sublinear, about $\frac{1}{2}$ mm long. Ovary globose. Style nearly glabrous, up to 13 mm long. Capsules unknown.

Holotype: *Ducke* RB 34671 in RB. Isotypes in: G, K, P, S, U, US.

Distribution: Upper Rio Negro.

BRAZIL, Amazonas: Rio Curicuriary, affl. Rio Negro, *Ducke* RB 34671; R. Ica, affl. Rio Negro, *R. L. Froes* 22377.

Ecology: The type-specimen was collected on rocky soils, the second one in "caatinga" forest on sandy soil.

Observation: This species was discovered by Ducke on an expedition organized by Colonel Themistocles Paes de Souza Brasil, head of the Brazilian eastern frontier commission.

18. **Qualea pulcherrima** Spruce ex Warm. Flora Bras. **13**(2): 37. 1875; *Ducke* 1938 p. 38.

Large tree. Branchlets and leaves glabrous, the cortex of the former exfoliating (smallish fragments). Stipular glands urceolar, prominent, mainly in the inflorescence, diameter about 1 mm. Petioles 8–14 mm long. Leaf-blades coriaceous, elliptic or oblong-elliptic, $6-9 \times 3-4$ cm; the apex long obtuse-acuminate, the base rounded or obtuse, the midrib not winged, the lateral nerves about 15 per cm, subprominent on both sides; veinlets inconspicuous. Inflorescence a loose panicle bearing 2–3 flowered cincinni, the slender pedicels subpuberulous, $(1-1\frac{1}{2})-2$ cm long. Flower-buds acute, about 10×5 mm. Calyx blue, adpressed greyish-pilose outside, the first minor lobe about 5–7 mm long, the other minor lobes 7–10 mm long, the spurred lobe obtuse or rounded, about 15–18 mm long; the spur subclavate, about 6–7 mm long, slightly constricted near the base, more or less stretched along the pedicel. Petal rose-pink, broadly obcordate, emarginate, up to 3 cm long and 4 cm wide. Anther recurved, subpuberulous, about 3 mm long; the filament slender, glabrous, about 7 mm long. Stami-

nodes — if present — about $\frac{1}{2}$ mm long. Ovary subglobose. Style glabrous except the base, 8–10 mm long. Capsules unknown.

Holotype: *Spruce* 3388 in C. Isotypes in: BM, BR, G, GH, GOET, F, K, NY, OXF, P, W.

Distribution: Upper Rio Negro.

BRAZIL, Amazonas: "Ad flumina Cassiquiari, Vasiva et Pacimoni", *Spruce* 3388; Rio Curicuriary, affl. Rio Negro, *Ducke* RB 34665.

COLOMBIA, Uaupes: *P. H. Allen* 3346.

Ecology: *P. H. Allen*: "frequently in areas of 'Rebalsa' which are flooded during the rainy season". *Ducke*: "In forests on high grounds".

19. ***Qualea gestasiana*** St. Hil. Mém. Mus. Paris **6**: 254. 1820; Spreng. 1825 p. 17; Schult. 1827 p. 99; DC. 1828 p. 28; A. Dietr. 1831 p. 99; Don 1832 p. 671; D. Dietr. 1839 p. 21; Warm. 1875 p. 54; — 1889 p. 23; Poulsen 1881 p. 112, 123; Wille 1882 p. 181 (anat.); Glaziou 1905 p. 31. *Qualea microphylla* Warm. l.c. p. 37.

Large tree. Branchlets and leaves glabrous or nearly so. Stipules triangular, about 1 mm long, the apex caducous, the base subglandular and subprominent; extrafloral nectaries above these glands, urceolar, about 3 mm high, the base about 1 mm wide. Petioles slender, about 7–12 mm long. Leaf-blades coriaceous, elliptic, broadly lanceolate or obovate-elliptic, $3-5 \times 1\frac{1}{2}-2\frac{1}{2}$ cm; the apex abruptly obtuse-acuminate; the base acute; the midrib winged; 30–40 lateral nerves per cm, minor and major ones only slightly different; veinlets only near the margin. Flowers fragrant, in few-flowered axillary racemes, the latter 2-, 4- or 6-flowered; the pedicels subpuberulous, slender, about as long as the buds, the latter about $9-13 \times 6-8$ mm. Calyx-lobes ciliate, the first one about 4 mm, the second one about 5–7 mm, the anterior ones 7–8 mm long; the spurred lobe about 15 mm long and wide, the outside of the base whitish-sericeous, the spur hidden between the other lobes, bag-shaped, about 2 mm long. Petal white (in sicc. yellow) with a yellow centre and painted with red above the base, obcordate, about 4×4 cm. Stamen glabrous, the anther recurved, acuminate and flattened, 6–7 mm long; the filament about 10 mm long. Rudimentary petals and staminodes — if present — about $\frac{1}{2}$ mm long. Style glabrous, about 1 cm long. Capsules about 4 cm long, the apex obtuse or rounded.

Holotype: *St. Hilaire* 72 near Tejuca, Rio de Janeiro in *P. Hilaire* of *Q. microphylla* Warm.: *Dux d'Abrantes* s.n. in *P.*

Distribution: In the forests around the town of Rio de Janeiro.

BRAZIL, Rio de Janeiro: *St. Hilaire* 72; *Dux d'Abrantes* s.n.; *Glaziou* nos 9416, 10731; *Ducke* RB 21289; *Kuhlmann* RB 48136; *Duarte de Barros* 53; *Nadeaud* s.n.

Ecology: In coastal forests on the atlantic slopes near Rio de Janeiro; fl. Febr.; up to 750 m.

Observation: *St. Hilaire* mentions as collectors of the type-specimen the Count de Gestas and the Countess de Roquefeuille. These names are not present on the type-sheet in Paris which bears a normal *St. Hilaire* label (*Voyage* 1816–1821). The species was named after the first collector.

20. ***Qualea homosepala*** *Ducke*, Arch. Inst. Biol. Veg. **4**: 38. 1938.

Large tree. Branchlets and leaves glabrous or nearly so, the cortex of the former not exfoliating. Stipules transversely elliptic with an

acute, caducuous apex and a glandular, persistent base. Petioles 9–13 mm long. Leaf-blades coriaceous, oblong or elliptic-oblong, $6\text{--}13 \times 3\text{--}6$ cm, the apex obtuse-acuminate, the base rounded; the midrib narrowly winged below; the lateral nerves subprominent, 20–30 per cm; the veinlets numerous. Inflorescence a panicle composed of racemes bearing 2–8 pairs of 2–3 flowered cincinni. Rachis, pedicels and bracts puberulous; the pedicels 5–7 mm long; the bracts and bracteoles caducous, transversely elliptic, rounded or obtuse, about $\frac{1}{2}$ –1 mm long. Flower-buds about 8–10 mm long, obtuse or rounded. Calyx-lobes dark pink-brownish, greyish sericeous outside; the minor lobes subequal, rounded or obtuse, up to 6–10 mm long; the spurred lobe broadly elliptic, about 15 mm long; the spur hidden by the lobes, straight, cylindrical, about 10–12 mm long. Petal pink, obcordate, emarginate, up to $3 \times 3\frac{1}{2}$ cm. Rudimentary petals and staminodes — if present — $\frac{1}{2}$ –1 mm long. Anther acute, about 4–5 mm long, greyish-puberulous on the back; the filament puberulous, about 10 mm long. Style nearly glabrous. Capsules unknown.

Holotype: *Ducke* RB 34666 in RB. Isotypes in: G, IAN, K, NY, P, S, U, US. Distribution: Upper Amazonia.

BRAZIL, Amazonas: Parintins, Lago José-assú, *Ducke* RB 34666.

COLOMBIA, Uaupès: Miraflores, *Gutierrez & Schultes* 530

Ecology: Type-specimen on high sandy grounds; fl. Dec.–Jan.

21. ***Qualea sprucei*** Warm. *Flora Bras.* **13**(2): 38. 1875.

Branchlets and leaves glabrous; the cortex of the former not ex-foliating. Stipular glands — if present — prominent; opposite stipules connected by a prominent stipular ridge. Petioles 6–10 mm long. Leaf-blades coriaceous, oblong or elliptic, $8\text{--}9 \times 2\frac{1}{2}\text{--}3\frac{1}{2}$ cm; the apex long and more or less abruptly acuminate ($1\text{--}1\frac{1}{2}$ cm); the base obtuse or rounded; the midrib pilose above, provided with ciliate wings below; 10–20 lateral nerves per cm; veinlets few, mainly near the margin. Inflorescence a many-flowered panicle bearing 1–3 flowered cincinni. Pedicels densely tomentellous, 6–8 mm long. Flower-buds acute, 3–10 mm long. Calyx, the spurred lobe in particular, densely greyish-sericeous outside; the minor lobes $5\text{--}6 \times 4\text{--}5$ mm; the spurred lobe suborbicular, emarginate, up to 8–12 mm long and wide; the spur up to 8 mm long, subclavate or subcylindrical, straight or slightly incurved. Petal obcordate, two-lobed, up to 3×3 cm, glabrous except the base. Anther glabrous, oblong, $1\frac{1}{2}\text{--}2$ mm long; the filament pilose, about 5 mm long. Staminodes oblong, up to 1 mm long. Style nearly glabrous. Capsules unknown.

Holotype: *Spruce* 2740 in C. Isotypes in: BM, BR, F, G, GH, GOET, K, NY, OXF, P, W.

Distribution: Once collected.

BRAZIL, Amazonas: Panuré on Rio Uaupès, *Spruce* 2740.

22. ***Qualea coerulea*** Aubl. *Pl. Gui.* 7. 1. 2. 1775; *Lam.* 1791 p. 11; *Willd.* 1797 p. 18; *Vahl* 1804 p. 6; *Pers.* 1805 p. 4; *Roem. & Schult.* 1817 p. 37; *Spreng.* 1825 p. 17; *Schult.* 1827 p. 99; *DC.*

1828 p. 28; A. Dietr. 1831 p. 98; Don 1832 p. 671; D. Dietr. 1839 p. 21; Warm. 1875 p. 33; — 1889 p. 22; Pulle 1906 p. 250; Benoist 1915 p. 242; — 1919 p. 319; — 1931 p. 165; Ducke 1922 p. 196; — 1938 p. 38; Pfeiffer 1926 p. 351; Amshoff 1948 p. 41; Mennega 1948 p. 45; Stafleu 1951 p. 192; Lindeman 1953 p. 116.

Large or medium-sized tree. Branchlets and leaves glabrous or nearly so. Stipules deltoid, acute, the apex deciduous, the base subglandular, elliptic, not prominent; extrafloral nectaries rarely present in the axils, about 1 mm high. Petioles 4–7 mm long. Leaf-blades coriaceous, elliptic, 6–9 × 3–4 cm; the apex acute or obtuse-acuminate; the base acute in youth; the midrib below provided with ciliate wings; 30–50 thin lateral nerves per cm, curved upwards near the margin, with the numerous veinlets forming a distorted reticulate venation near the margin. Fragrant flowers in many-flowered compound racemes bearing 1–3 flowered cincinni. Pedicels 4–8 mm long, subpuberulous. Flower-buds 5–8 mm long. Calyx subsericeous outside, the minor lobes rounded or obtuse, 3–5 mm long; the spurred lobe 7–8 × 9–11 mm, emarginate; the spur cylindrical, slender, 5–6 mm long. Petal blue with a yellow base, obcordate, deeply emarginate, about 1½–2½ cm long and wide. Stamen glabrous, the anther about 2 × 1 mm, apically recurved; the filament slender, up to 8 mm long. Staminodes and rudimentary petals sometimes present, ½–1 mm long. Style entirely glabrous, 5–7 mm long. Capsules 6–7 cm long, the exocarp coming off.

Holotype: *Aublet* s.n. in BM.

Distribution: French Guiana, Suriname, Para and Maranhao.

BRAZIL, Para: Belem, *N. F. da Silva* 135; Rio Tapajoz, *Ducke* PG 16455 = RB 8420; Rio Anajaz, *Ducke* RB 17775; Belem, *Archer* 7878; Beira do Rio Irituia, *Black & Forster* 48–3348. Maranhao: Carutapera Region, *Froes-Krukoff* 2029.

SURINAME: Numerous collections; for detailed numbers, etc. cf. Stafleu 1951 p. 193.

FRENCH GUIANA: Numerous collections by *Mélinon*, *Sagot*, *Wachenheim*, *Benoist*, e.g.: Maroni, *Mélinon*, 47, 105; Karouany, *Sagot* 981; *Aublet* s.n.; Gourdonville, *Benoist* 1604.

Ecology: In forests within and outside the range of seasonal floods; fl. Sept.–Dec.; fr. Dec.–March.

Vernacular names: BRAZIL, Para: Páu de Mastro; Maranhao: Guiariuba. FRENCH GUIANA: Couaie. SURINAME: Watra kwarrie (Surinam); Muneridang (Arawak); Jakopi or Iriakopi (Caraib); for a complete list of French Guiana and Suriname names cf. Stafleu 1951 p. 194.

23. ***Qualea impexa*** Macbr. Field Mus. Bot. **11**: 67. 1931; — 1950 p. 878.

Medium-sized tree. Branchlets glabrous, the cortex not exfoliating. Stipules broadly deltoid, acute, about 1 × 1 mm, the apex caducous, the base persistent and subglandular; those of opposite leaves connected by a straight stipular ridge. Petioles 9–13 mm long. Leaf-blades glabrous, elliptic or suboblong, up to 11 × 5 cm; the apex shortly obtuse-acuminate (4–10 mm); the base abruptly contracted towards the petiole; the midrib below provided with two narrow ciliate wings; more than 30 lateral nerves per cm; veinlets numerous on the entire

surface. Inflorescence a many-flowered panicle composed of 1–2 flowered cincinni. Pedicels subpuberulous, 9–13 mm long. Flowerbuds $1\frac{1}{2}$ –2 cm long, subacute. Calyx greyish-subsericeous outside, especially the inner lobes; the minor lobes subequal, about $8\text{--}12 \times 7\text{--}12$ mm; the spurred lobe broadly elliptic, about $1\frac{1}{2}\text{--}2 \times 1\frac{1}{4}\text{--}1\frac{1}{2}$ cm; the spur bag-shaped, constricted near the base, about 4–6 mm long. Petal yellow, cordate, about 4×5 cm. Stamen glabrous; the anther 8–9 mm long; the filament about 11–14 mm long. Staminodes, if present, linear, about 1 mm long. Ovary gradually merging into the glabrous style. Capsules unknown.

Holotype: *G. Klug* 748 in F. Isotypes in: G, US.

Distribution: Once collected.

PERU, Loreto: Mishuyacu near Iquitos, *G. Klug* 748.

Ecology: In forest, 100 m.; fl. Jan.

Observation: Differs from *Q. schomburgkiana* by the presence of a stipular ridge, by the numerous veinlets on the entire surface and by the yellow petal: from *Q. lineata* for instance by the equal lateral nerves and also by the yellow petal.

24. ***Qualea acuminata*** Spruce ex Warm. Flora Bras. **13**(2): 40. 1875; Petersen 1896 p. 318. *fig. 172 M*; Benoist 1915 p. 242; — 1931 p. 163; Ducke 1933 p. 44; — 1938 p. 40; Stafleu 1951 p. 194. *Qualea speciosa* Huber 1902 p. 425; Ducke 1915 p. 49; — 1922 p. 197.

Large or medium-sized tree. Branchlets subpuberulous or glabrous, the cortex not exfoliating. Stipular glands prominent, about 1 mm long. Petioles 2–9 mm long. Leaf-blades glabrous, coriaceous, oblong or elongate-elliptic, $8\text{--}18 \times 3\frac{1}{2}\text{--}4\frac{1}{2}$ cm; the apex long acute-acuminate ($\frac{1}{2}\text{--}1\frac{1}{2}$ cm); the base truncate, rounded or subcordate; the midrib not or narrowly winged below, the wings puberulous; 30–45 lateral nerves per cm; veinlets few, mainly near the margin. Inflorescence a raceme or panicle composed of 1–2 flowered cincinni; the pedicels 5–10 mm long, pubescent. Flowers fragrant, the buds 15–23 mm long, acute. Minor calyx-lobes purplish, sericeous outside, the first one about 6 mm, the other ones about 7–11 mm long; the spurred lobe densely sericeous outside, up to $2\frac{1}{2} \times 2$ cm; the spur 7–10 mm long, constricted near the base. Petal white with a red basal spot and a yellow central strip, obcordate, 4–5 cm long and wide. Stamen glabrous; the anther 9–11 mm long, apically recurved and acute; the filament firm, 8–11 mm long. Staminodes, if present, linear, up to 3 mm long. Ovary gradually merging into the style; the latter 10–14 mm long, glabrous except the lower 2–3 mm. Immature capsule about 3 cm long, rugulose.

Lectotype: *Spruce* 2612 in C. Isotypes in: BM, BR, F, GH, GOET, K, NY, OXF, P, W. Holotype of *Q. speciosa* Huber: *Huber* 1844 in PG, isotype in G.

Distribution: Throughout the entire Amazonian basin.

BRAZIL, Para: Gurupa, *Ducke* PG 15978; —, — RB 17761; Rio Mojù, *Ducke* RB 17762; Almeirim, *Ducke* PG 17286 = RB 13698; Rio Tucuruhy, *Ducke* PG 16593 = RB 13699; Tomé Assu, *Mexia* 5973a; —, *J. M. Pires* 1441; Arama, *Huber* PG 1844. Amazonas: Manáos, *Ducke* RB 23488; —, — 55; —, *Killip & Smith* 30204; near Panuré on Rio Uaupès, *Spruce* 2612; Humayta, *Krukoff* 7169; Rio Iá, *Froes* 22378; Sao Paulo de Olivença, *Krukoff* 8949; Rio Icana, *Black* 48–2664; Rio Solimoes, *Froes* 23760.

COLOMBIA, Uaupès: Yurupari, *Cuatrecasas* 6956.

BOLIVIA, Beni: Rio Ibon, *Cardenas* 2083.

FRENCH GUIANA: *Leprieux* s.n.; — 284.

Ecology: In forests on high grounds as well as on grounds reached by seasonal floods; fl. mainly Sept.–Feb., sometimes later.

Vernacular names: Para: Mirabau do Varzea.

Observation: It is not possible to say which of the Spruce 2612 specimens was Warming's holotype.

25. ***Qualea elegans*** Taub. ex Benoist in Lecomte, Not. Syst. **3**: 177. 1915; Taub. ex Glaziov 1905 p. 30 nomen nudum.

Shrub. Branchlets puberulous in youth, glabrous in age, the cortex not exfoliating. Stipules broadly elliptic, about 1 mm long and 2 mm wide at the base, apiculate. Glands single or in serial pairs in the axils of the stipules, crateriform, up to 1 mm wide. Stipular ridge weak. Petioles 2–4 mm long. Leaf-blades glabrous above, slightly hairy below (in youth) especially on the wings of the midrib, rigidly coriaceous, ovate or elliptic-ovate, up to 10×5 cm, the apex obtuse or somewhat rounded, the base rounded or cordate; 10–20 subprominent slightly curved lateral nerves per cm; veinlets on the entire surface; the margin subrevolute. Inflorescence a few-flowered raceme composed of opposite 1(–2) flowered cincinni. Pedicels puberulous, firm, 14–18 mm long. Flower-buds acute, about 20 mm long. Calyx subpuberulous outside, the minor lobes subequal, rounded, 7–12 mm long; the spurred lobe elliptic, rounded or obtuse, $2-2\frac{1}{2}$ cm long; the spur hidden by the lateral lobes, bag-shaped, about 4×3 mm, pressed against the back of the fourth lobe. Petal “white-yellowish”. Stamen glabrous; the anther acute, linear-oblong, 10–12 mm long; the filament 6–10 mm long. Staminalodes, if present, linear, about 1 mm long. Ovary gradually merging into the glabrous style. Capsules unknown.

Holotype: *Glaziov* 19153 in P. Isotypes in: C, F, K, S.

Distribution: Once collected.

BRAZIL, Minas Geraes: Biribiri near Diamantina, *Glaziov* 19153, fl. March–April.

26. ***Qualea calantha*** Pilger, Notizbl. Berlin **11**: 297. 1931; Macbride 1950 p. 876.

Tree of medium size. Branchlets glabrous, the cortex not exfoliating. Stipular glands subprominent, connected by a V-shaped stipular ridge. Petioles firm, about 10 mm long. Leaf-blades glabrous, rigidly coriaceous, elliptic or elliptic-oblong, about 11×5 cm; the apex long-acuminate; the base rounded; more than 10 lateral nerves per cm, curved upwards near the margin; veinlets numerous, mainly near the margin. Inflorescence an up to 13 cm long many-flowered panicle composed of 1–2 flowered cincinni. Pedicels puberulous, 7–10 mm long. Flower-buds acute, about 15 mm long. Minor calyx-lobes rounded, subpuberulous, ciliate, subequal, 8–10 mm long; the spurred lobe 13–16 mm long, the base bag-shaped, not spurred. Petal white with a yellow centre and a pink base, cordate-obovate, deeply two-lobed, up to $5\frac{1}{2}$ cm long. Anther oblong, about 8 mm long, shortly

apiculate; the filament about 12 mm long. Staminodes, ovary, style and capsules unknown.

Holotype: *Tessmann* 4855 in B, now destroyed. No duplicate is known to the present author. Photograph in GH.

Distribution: Eastern Peruvia.

PERU, Loreto: Pongo de Manseriche, *Tessmann* 4855.

Ecology: On slopes in virgin forest, 30 m above water level, 160 m.; fl. Dec.

Observation: The above description is based on Pilger (l.c.) and on the GH photograph. The species, which seems to be a good one, is closely related to *Q. macropetala*. It is characterised by the bag-shaped base of the fourth calyx-lobe (no spur), the small flowers and the ample raceme. Further material should be examined.

27. ***Qualea ingens*** Warm. *Flora Bras.* **13**(2): 40. 1875; Hochne 1951 p. 257.

var. ***ingens*** (*fig. 2a*)

Large tree. Cortex of the young branchlets exfoliating. Stipules caducous, triangular, $\frac{1}{2}$ –1 mm long and about 1 mm wide; crateriform glands in the axils; those of opposite leaves connected by a straight, prominent stipular ridge. Petioles about 10 mm long. Leaf-blades coriaceous, complicate, elliptic-oblong or subelliptic, 10–14 \times 4–7 cm; the apex obtuse-acuminate or subobtuse; the base cordate; the midrib winged below; more than 50 lateral nerves per cm, curved upwards near the margin; veinlets numerous on nearly the entire surface. Inflorescence a many-flowered panicle composed of 1–2 flowered cincinni. Pedicels puberulous or glabrous, about 5 mm long. Flower-buds acute, up to 18 mm long. Calyx nearly glabrous outside, the minor lobes subequal, obtuse, 6–9 \times 4–7 mm; the spurred lobe ovate, up to 18 \times 15 mm; the spur irregularly bag-shaped, about 7 \times 4 mm, the apex rounded, the base constricted, often slightly compressed. Petal “coeruleous”. Anther acute, subrecurved, pilose on the back, about 7 mm long; the filament 12–15 mm long. Staminodes, if present, linear, about 1 mm long. Style glabrous. Capsules unknown.

Holotype: *Riedel* s.n. in C. Isotypes in: BM, G, GH, K, NY, OXF, P.

Distribution: Once collected.

BRAZIL, Matto Grosso: along Rio Aterrado between Cuyaba and Diamantino, *Riedel* s.n.

Ecology: “In humidis ad rivulum”, probably in the so-called cabeceiras, i.e. swampy river sources (cf. Ducke 1922 p. 197) as *Q. wittrockii* Malme (no. 5); fl. Sept.

var. ***duckei*** Staffl. nov. var.

Arbor magna, cortice ramulorum juvenilium fusco. Stipulae 1–2 mm longae, eae foliorum oppositorum basibus linea prominula curvata ramulum transiente connexis; glandulae axillares adsunt. Lamina basi rotundata. Petalum coeruleum lineis luteis, obcordatum.

Holotype: *Ducke* PG 15795 = RB 5725 in U. Isotypes in: BM, G, IAN, P, RB, US.

Distribution: Once collected.

BRAZIL, Para: Rio Cauhy, *Ducke* PG 15795 = RB 5725.

Ecology: In marshy forests, together with *Q. wiltrockii* Malme (no. 5); fl. Oct.

Observation: Differs from the var. *ingens* by the curved stipular ridge and the shape of the leaf-base. Ducke (1922 p. 196, 1938 p. 39) mentioned the variety sub: "*Qualea ingens* Warm. var. (vel spec. nova affinisima)".

28. ***Qualea amoena*** Ducke, Arch. Jard. Bot. Rio 3: 197. 1922; — 1938 p. 41.

Large tree. Branchlets subpuberulous in youth, the cortex exfoliating. Stipules acute, $\frac{1}{2}$ –1 mm long, connected with another by a V-shaped subprominent stipular ridge, axillary extrafloral nectaries up to 2×2 mm, irregularly urceolar, thin-walled, the base constricted. Leaf-blades coriaceous, lanceolate-oblong or rarely elliptic-oblong, up to 10×3 cm; the apex gradually and long acuminate (about 10 mm); the base obtuse; the midrib subpuberulous and winged below; about 10 major lateral nerves per cm, 2–4 slightly weaker ones in between each pair; numerous veinlets on the entire surface. Inflorescences many-flowered panicles composed of 1–2 flowered cincinni. Pedicels 7–10 mm long, puberulous. Flowers fragrant, the buds 12–15 mm long. Calyx sericeous outside, the minor lobes about half as long as the spurred one, rounded, the first one about 6 mm, the other ones 8–12 mm long; the spur ellipsoid, $6-7 \times 4-5$ mm. Petal white with a yellow centre and red spots near the base, about $4 \times 4\frac{1}{2}$ cm. Rudimentary petal and staminodes present. Anther glabrous or with a few hairs on the back, subrecurved, lanceolate, about 9 mm long; the filament glabrous, about 12–14 mm long. Style glabrous. Capsules unknown.

Holotype: Ducke PG 15890 = RB 8345 in PG. Isotypes in: F, G, IAN, K, P, RB, U, US. Photograph of PG type in F.

Distribution: Central Amazonian basin.

BRAZIL, Para: Salgado lake, Ducke PG 15890 = RB 8345. Amazonas: Humayta on Rio Madeira, Krühlf 6433 and 6575; Esperança, Rio Javary, Ducke 1063.

Ecology: On terra firma; fl. Oct.–Dec.

29. ***Qualea rosea*** Aubl. Pl. Gui. 5. t. 1. 1775; Lam. 1791 p. 11. t. 4; Willd. 1791 p. 18; Poir. 1804 p. 8; Vahl 1804 p. 6; Pers. 1805 p. 4; Roem. & Schult. 1817 p. 36; Spreng. 1825 p. 17; DC. 1828 p. 28; A. Dietr. 1831 p. 97; Don 1832 p. 671; D. Dietr. 1839 p. 21; Warm. 1875 p. 54, — 1889 p. 23; Benoist 1915 p. 242, — 1919 p. 319; — 1931 p. 163; Berlin 1920 p. 81; Stafleu 1951 p. 194. *Qualea violacea* Mart. & Zucc. ex Schult. 1827 p. 99 (in synonym.) *Qualea melinonii* Beckmann 1908 p. 280.

Tree of medium size. Branchlets glabrous, the cortex exfoliating. Stipules about 1 mm long, connected by a stipular ridge; extrafloral nectaries in the axils, mostly urceolar or conical, about 2 mm high, about 1 mm wide, thin-walled. Petioles 7–15 mm long. Leaf-blades glabrous, firmly coriaceous, the margin dark when dry, broadly elliptic, oblong or ovate-oblong, $7-11 \times 3\frac{1}{2}-6$ cm; the apex shortly obtuse-acuminate; the base rounded or obtuse in age, obtuse in youth; the midrib below provided with two narrow wings; more than 20

lateral nerves per cm; veinlets numerous on the entire surface. Panicle few-flowered. Cincinni 1(-2) flowered, at the base provided with bracts, stipules and nectaries. Pedicels subpilose, 1-1½ cm long. Flowers fragrant, the buds 12-17 mm long. Minor calyx-lobes more or less rounded, puberulous, the first one 5 mm, the others 7-9 mm long; the spurred lobe suborbicular, emarginate, up to 17 mm long, sericeous outside, glabrous and pinkish inside; the spur bag-shaped, slightly inflated or somewhat depressed, 4-7 × 3-5 mm, before anthesis hidden between the outer calyx-lobes. Petal yellow with a whitish base, suborbicular-obcordate, about 3-3½ × 3-3½ cm. Anther recurved, lanceolate, subapiculate, 6-8 mm long, the centre of the back pilose or nearly glabrous; the filament glabrous, up to 15 mm long. Staminodes and rudimentary petals linear, 1-2 mm long. Style glabrous except the basal 1 mm. Capsules up to 9 cm long, the exocarp 5-8 mm thick, woody, the outer surface dull, rugulose and glabrous, releasing from the ½-1 mm thick, shining endocarp; up to 10 seeds per locule.

Holotype: *Aublet* s.n. in BM. Holotype of *Q. melinonii* Mélinon (1863) s.n. in B, now destroyed (photograph in F); isotypes in: BM, NY, P, US.

Distribution: French Guiana and Suriname.

SURINAME: Brownsberg, tree 1008 *B.W.* nos. 1761, 4260, 6336, tree 1168 *B.W.* 2479; Moengo Tapoe, *Lanjouw & Lindeman* 392, 395; Nassau Mountains, *Lanjouw & Lindeman* 2440, 2802, 2920; *B.B.S.* 171.

FRENCH GUIANA: Maroni, *Mélinon* s.n.; —, Gandoger 100; Charvein, *Benoist* 187; Godebert, *Wachenheim* s.n.; *Mélinon* (1863) s.n.; *Poiteau* s.n.

Ecology: In high primeval forests which are not reached by seasonal floods; fl. Sept.-Dec.; fr. Febr.-March.

Vernacular names: (for a complete list cf. Stafleu 1951 p. 196) SURINAME: Bergkwarrie, Gronfoloe (Surinam), Gronfoloe, Muneridang (Arawak); Iriakopi (Caraib). FRENCH GUIANA: Cèdre jaune, Cèdre gris.

Use: Bertin (l.c.) mentions the use as a lumber tree in French Guiana.

30. *Qualea lineata* Staff. nov. spec. (fig. 10).

Subgenus *Qualea*, sectio *Qualea*. Arbor magna. Ramuli juveniles subpuberuli. Stipulae late ovatae, acuto-acuminatae, 1-2 mm latae, basi incrassatae; eae foliorum oppositorum basibus linea prominula ramulum transiente connexis. Glandulae in axillis stipularum circa 1 mm latae. Petiolus 1-6 mm longus. Lamina glaberrima, oblonga vel elliptico-oblonga, ad 10 × 4½ cm, apice breviter (4-8 mm) acuminata, basi rotundata; costa subtus hialata et subpuberula; nervis lateralibus majoribus 8-20 per cm, inter se venulis transversalibus creberrimis junctis. Inflorescentia thyrsoidae; cincinnis unifloris; pedicellis puberulis 10-15 mm longis, circa ½ mm latis. Alabastra conica, subacuta, 14-18 mm longa. Calycis laciniae sericeae, in vivo virescente-roseae, minores subequales, subellipticae, rotundatae, circa 8-13 mm longae et 7-11 mm latae; lacinia major subovata vel suborbicularis, ad 20 × 20 mm. Calcar ellipsoideum, sub anthesi laciniis calycis lateralibus obtectum, basi subconstrictum. Petalum roseum vel roseo-luteum, medio purpureum. Stamen glabrum; anthera oblonga apice obtusa, circa 8 mm longa. Staminodia linearia, ½-1 mm longa. Basis styli (2-3 mm) puberula. Capsula ignota.

Holotype: *Cuatrecasas* 14410 in U. Isotype in US.

Distribution: Once collected.

COLOMBIA, Del Valle: Cordillera occidental, between Pavas and Miramar, *Cuatrecasas* 14410.

Ecology: 350-450 m.; fl. Apr.

Observation: Characterised by the major and minor lateral nerves, the stipular ridge, the numerous veinlets, etc. Nearest related to *Q. schomburgkiana* (no. 39) and *Q. impexa* (no. 23).

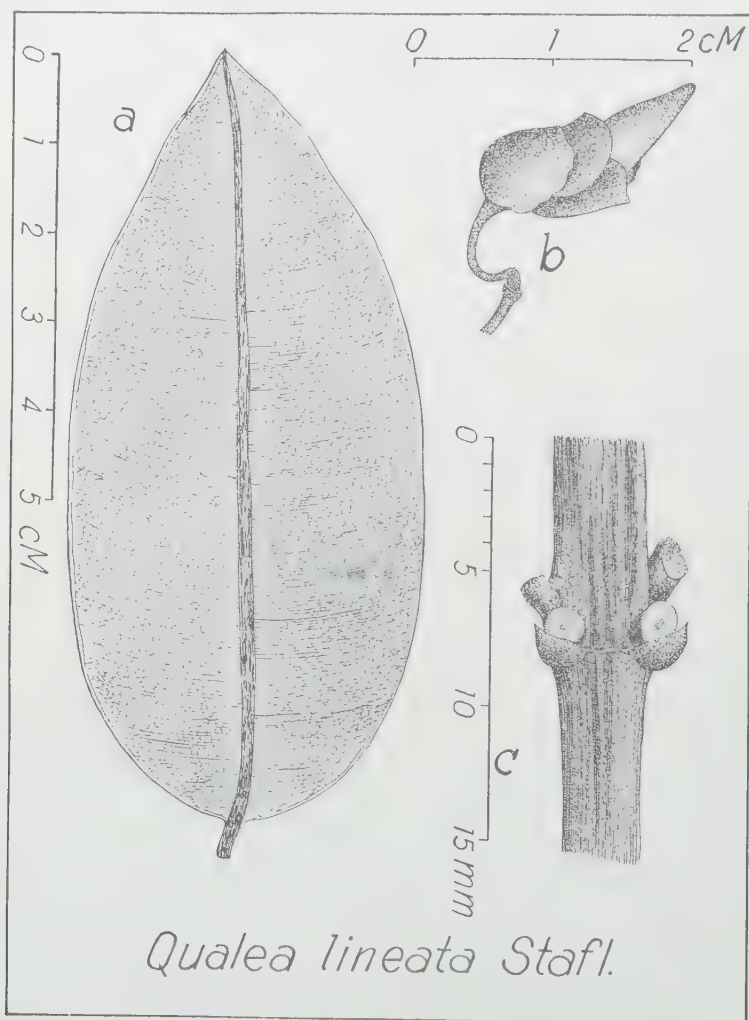


Fig. 10. *Qualea lineata* Stapf. a. Leaf; b. flower-bud; c. stipules and axillary glands.

31. ***Qualea polychroma*** Stapf. nov. spec. (fig. 11).

Subgenus *Qualea*, sectio *Qualea*. Arbor magna. Ramuli glabri, decorticantes, cortice nigro. Stipulae subovatae; basi incrassata et haud decidua; apice acuto et deciduo; basibus linea prominula

ramulum transiente connexis. Petiolus 5–9 mm longus. Lamina glabra, elliptica vel elliptico-oblonga, 9–13 cm longa et $3\frac{1}{2}$ – $4\frac{1}{2}$ cm lata; apice breviter acuto-acuminata; basi retundata; costa subtus bialata; nervis lateralibus ultra 20 per cm, inter se venulis transversalibus creberrimis junctis. Inflorescentia thyrsoides, cincinnis 1–2 floris, pedicellis puberulis, 8–11 mm longis. Alabastra 12–16 mm longa. Calycis lacinae intus rufo-brunneae, extra nigrae, sericeae, minores 7–13 mm longae;

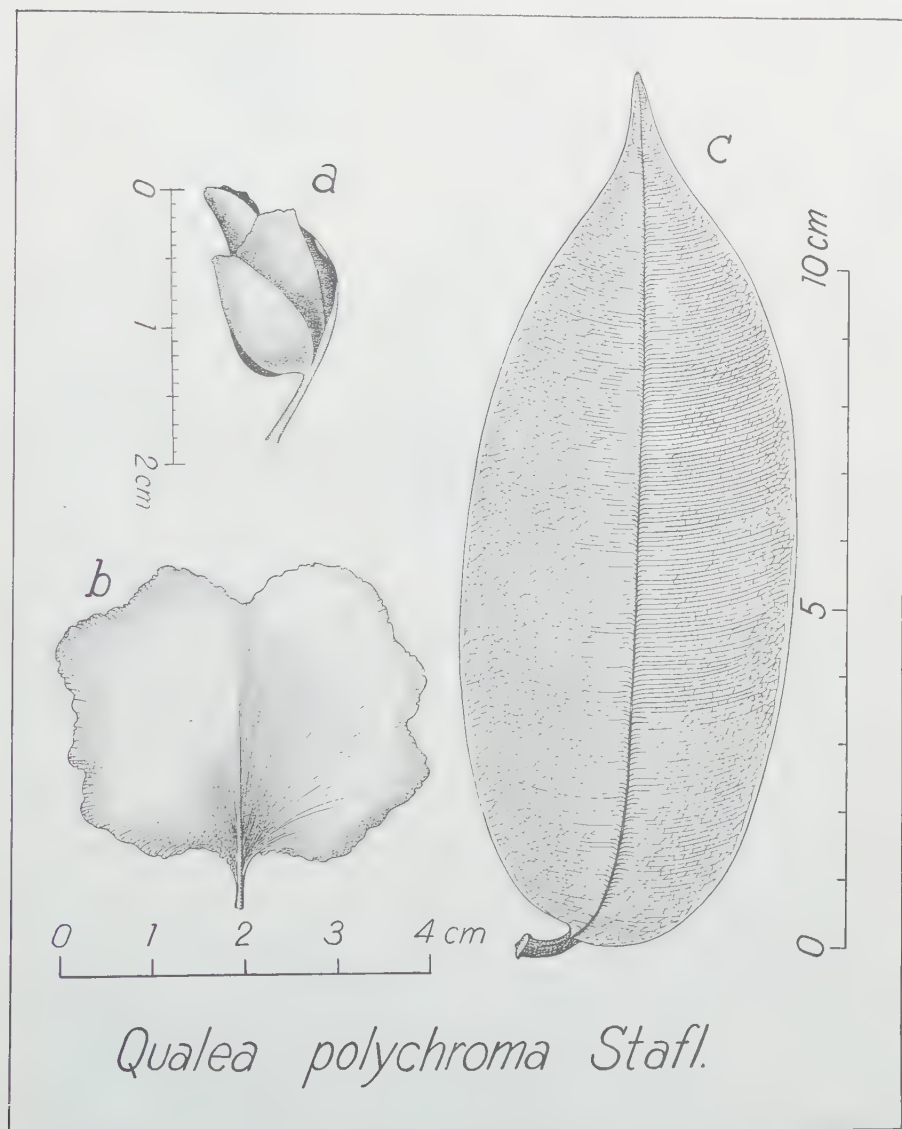


Fig. 11. *Qualea polychroma* Stafl. a. Flower-bud; b. petal; c. leaf.

lacinia major caduca, expansa non vidi. Calcar cylindricum, caducum, circa 6 mm longum. Petalum roseo-rubescens medio lineis flavis notatum, late ellipticum, emarginatum, ad 3 cm longum et $4\frac{1}{2}$ cm latum. Anthera nigra pilosa, lineari-oblonga, acuta, 4–5 mm longa. Filamentum roseo-rubescens, pilosum, circa 10 mm longum. Staminodia vel (et) petala rudimentaria circa 1 mm longa. Stylus glaber, ruber, circa 1 cm longus, stigmatibus capitato. Capsula ignota.

Holotype: *Forest Dept. Brit. Guiana* 2832 in K.

Distribution: Once collected.

BRITISH GUIANA: Slopes of Mount Roraima, Arabupu, *Forest Dept. Brit. Guiana* 2832 in K.

Ecology: "In mixed forest on clay soil, 4600 feet".

Observation: The species is characterised by the exuberantly coloured flowers, the pilose filament and anther, the stipular ridge, etc.

32. ***Qualea macropetala*** Spruce ex Warm. *Flora Bras.* **13**(2): 41. t. 6 fig. 1. 1875.

Tree. Branchlets glabrous, the cortex more or less exfoliating; a callous margin around the cicatrices of the leaves. Stipular glands subconspicuous. Petioles about 1 cm long. Leaf-blades glabrous, rigidly coriaceous, broadly elliptic or subovate, 9–12 × 5–6 cm; the apex abruptly acuminate, up to 1 cm long; the base rounded, often somewhat folded; the midrib not winged; more than 10 lateral nerves per cm; veinlets numerous on the entire surface. Inflorescence a dense panicle composed of 1–2 flowered cincinni. Pedicels pubescent, up to 14 mm long. Flower-buds acute, about 2 cm long. Calyx, in particular the inner lobes, sericeous outside, the lobes rounded, the first one 7–8 mm, the second and third ones 9–12 mm, the fifth one 10–13 mm, the elliptic fourth one 2–2½ cm long; the spur 8–10 × 3–5 mm, somewhat compressed, constricted near the base. Petal obcordate, emarginate, up to 6 × 8 cm, glabrous except the back of the base. Anther pilose on the back, apically obtuse and subrecurved, 7–10 mm long; the filament firm, densely pilose, up to 14 mm long. Style glabrous except the basal 1–2 mm. Capsules unknown.

Holotype: *Spruce* 2713 in C. Isotypes in: BM, BR, F, G, GH, GOET, K, NY, OXF, P, W.

Distribution: Once collected.

BRAZIL, Amazonas: Near Panuré on Rio Uaupès, *Spruce* 2713.

Observation: The specimen mentioned by Ll. Williams (1947 p. 91) belongs to *Q. schomburgkiana* Warm.

33. ***Qualea brevipedicellata*** Stafl. nov. spec. (*fig. 12*).

Subgenus *Qualea*, sectio *Qualea*. Arbor magna. Ramuli et folia glabri. Glandulae in axillis stipularum minutarum, callo-marginatae. Petiolus circa 10 mm longus. Lamina coriacea, elliptico-oblonga, 6–8 cm longa et 3–4 cm lata, apice subacuminata, basi abrupte in petiolum attenuata; costa subtus vix alata; nervis lateralibus ultra 20 per cm, inter se venulis transversalibus frequentis junctis. Inflorescentia thyrsoides, brevis, densiflora; cincinnis uni- vel rarius bifloris; pedicellis dense rufo-pubescentibus, crassis, 4–5 mm longis. Alabastra subovoidea,

circa 13–16 mm longa. Flores fragrantēs. Calycis laciniae extra dense rufo-sericeae, minores subequales, rotundatae, 8–12 mm longae; lacinia major late elliptica, rotundata, ad 16 mm longa. Calcar ellipsoideum, apice rotundatum, 6–8 mm longum, sub anthesi laciniiis calycis lateralibus obtectum. Petalum extra pilosum, suborbiculare, emarginatum, album medio luteum, versus basim maculae rufae

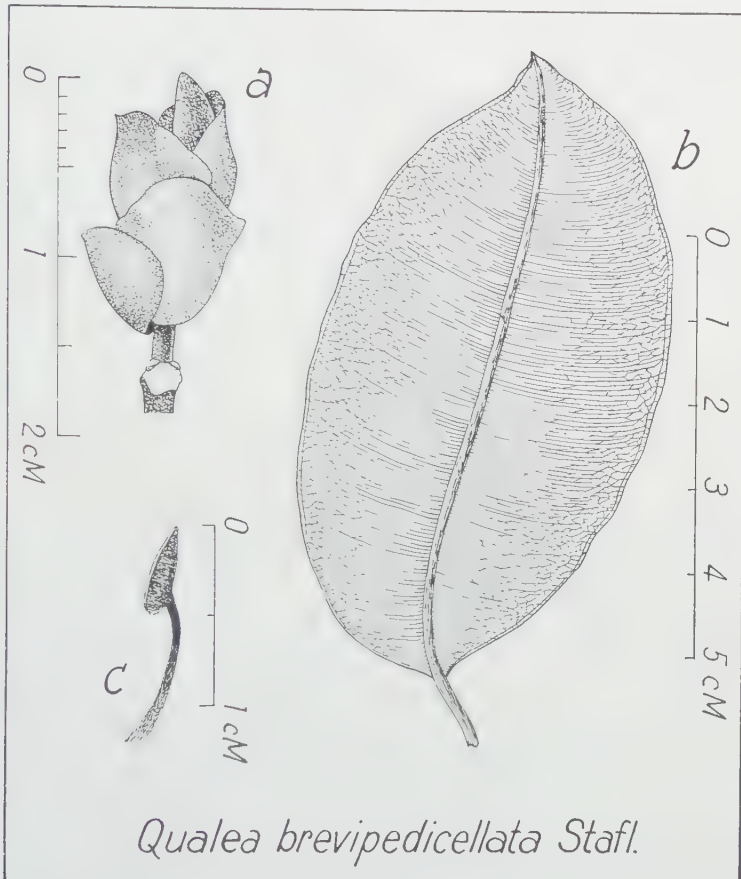


Fig. 12. *Qualea brevipedicellata* Staf. a. Flower-bud; b. leaf; c. stamen.

duabus notatum, basi unguiculata circa 8 mm longa. Petalum rudimentarium petaloideum, oblongum, apiculatum, circa 2 mm longum. Anthera dorso pilosa, apiculata, circa 5 mm longa, connectivo angusto. Filamentum dense pilosum, 12–14 mm longum. Staminodia linearia vel subulata, circa $\frac{1}{2}$ mm longa. Stylus glaber. Capsula ignota.

Holotype: *Ducke* 668 in F. Isotypes in: IAN, MO, NY, US.

Distribution: Once collected.

BRAZIL, Amazonas: Manaus, Estrada do Aleixo, *Ducke* 668.

Ecology: In forest on terra firma; fl. Jan.

Observation: Differing from *Q. gracilior* and *Q. paraensis* by the short pedicels, the structure of the stamen, the nervation of the leaves, etc.

34. ***Qualea tricolor*** Benoist in Lecomte, Not. Syst. **3**: 176. 1915; Benoist 1931 p. 164; Stafleu 1951 p. 195.

Large tree. Cortex of the branchlets exfoliating (small fragments). Stipules with acute deciduous apex and subglandular persistent base. Petioles about 5 mm long. Leaf-blades subcoriaceous, glabrous except the midrib, elliptic, up to $5 \times 2\frac{1}{2}$ cm; the apex obtuse-acuminate; the base acute; the midrib pilose below, hardly winged; 15–35 slightly curved lateral nerves per cm; veinlets few, only near the margin. Racemes composed of 1–2 flowered cincinni. Pedicels puberulous, up to 13 mm long. Flower-buds about 18 mm long. Calyx sericeous outside, the lobes rounded or obtuse, the minor ones $6\text{--}10 \times 4\text{--}7$ mm, the spurred lobe 15–17 mm long, the spur nearly glabrous, subcylindrical, slightly constricted near the base, 7–8 mm long, in youth ovoid and hidden between the lobes. Petal white with a yellow base and two red spots, suborbicular, subemarginate, up to 4×4 cm. Anther pilose on the back, apically truncate, 7–9 mm long; the filament glabrous, 10–12 mm long. Rudimentary petals petaloid, 3–5 mm long. Staminodes linear, about 1 mm long. Style glabrous. Capsules unknown.

Holotype: Benoist 1564 in P. Cotype: Mélinon 142 (1842) in P; duplicates in L and US.

Distribution: French Guiana.

FRENCH GUIANA: Gourdonville, Benoist 1564; Mélinon 142 (1842).

Ecology: Fl. Aug.

35. ***Qualea gracilior*** Pilger, Notizbl. Berlin **11**: 296. 1931; Ducke 1943 p. 18; Macbride 1950 p. 877. *Qualea lancifolia* Ducke 1935 p. 53; — 1938 p. 41.

Large tree. Young branchlets pubescent. Stipules acute-acuminate; axillary glands suburceolar, about 1 mm wide. Petioles 5–8 mm long, densely tomentose above. Leaf-blades coriaceous, $7\text{--}11 \times 2\frac{1}{2}\text{--}3\frac{1}{2}$ cm, lanceolate or lanceolate-oblong; the apex gradually and long acuminate (1 cm), obtuse and mucronulate; the base rounded or obtuse; the upper surface tomentose on the midrib, subpuberulous on the limb; the lower surface puberulous, the midrib hirsute on the narrow wings; 4–7 major lateral nerves per cm, 1–3 minor ones and many veinlets in between each pair, the nervation elegantly reticulate. Inflorescence a dense panicle composed of 1–2 flowered cincinni. Pedicels 6–8 mm long, densely pubescent. Flowers not fragrant; the buds about 13–17 mm long. Calyx densely sericeous outside, the minor lobes rounded, the lateral ones 6–9 mm, the anterior ones 9–12 mm long; the spurred lobe 15–17 mm long, rounded and emarginate; the spur ellipsoid, constricted near the base, glabrous, 5–7 mm long. Petal white, painted with yellow and red, the apex two-lobed, about 3 cm long and 5 cm wide. Anther pilose on the back or nearly glabrous, 8–10 mm long, the locules narrow and marginal on the 2 mm wide connective, the apex distinctly two-lobed and often recurved; the filament glabrous, 10–12 mm long. Style nearly glabrous. Capsules unknown.

Holotype: *Tessmann* 4465 in B, photographs in F and GH. No duplicate of the *Tessmann* type is known to the present author. The original is now destroyed and if no other specimens have been preserved it will be necessary to consider the photograph as the lectotype. Holotype of *Q. lancifolia* Ducke: *Ducke* RB 24160 in RB; isotypes in: K, NY, P, S, U, US.

Distribution: Eastern Peru and Upper Amazonia.

BRAZIL, Amazonas: Sao Paulo de Olivença, Rio Solimoes, *Ducke* RB 24160; Esperança on Rio Javary, *Ducke* 1064.

PERU, Amazonas: Upper Marañon, mouth of Rio Santiago, *Tessmann* 4465.

Ecology: In forests which are not reached by seasonal floods; fl. Oct.–Nov.

36. ***Qualea paraensis*** Ducke, Arch. Jard. Bot. Rio 1: 48, t. 16. 1915; *Ducke* 1922 p. 197; — 1938 p. 40; *Pilger* 1931 p. 296; *Macbride* 1950 p. 878.

Large tree. Cortex of the young branchlets exfoliating. Stipules acute, $\frac{1}{2}$ –1 mm long. Extrafloral nectaries in the axils of the stipules, urceolar, diam. about 1 mm, 1–2 mm high, the wall thin, the base somewhat constricted. Petioles 1–1 $\frac{1}{2}$ cm long. Leaf-blades coriaceous, oblong or elliptic-oblong, 5–11 \times 3–4 $\frac{1}{2}$ cm; the apex abruptly acuminate (4–8 mm); the base obtuse or acute; the midrib puberulous and narrowly winged below; about 8–15 major lateral nerves per cm, minor ones and numerous veinlets in between. Inflorescence composed of panicles bearing mostly 2-flowered cincinni. Pedicels puberulous, 4–8 mm long. Flowers fragrant, the buds 15–18 mm long. Calyx sericeous outside, in particular the inner lobes; the lobes rounded, the lateral ones 5–8 mm, the anterior ones 8–12 mm, the spurred one up to 18 mm long; the spur ellipsoid, 4–7 mm long. Petal white with a red base and a yellow centre, about 3 $\frac{1}{2}$ –4 $\frac{1}{2}$ cm long and wide. Anther lanceolate, about 7–9 mm long, subrecurved, the back pilose, the apex rounded and emarginate; the filament glabrous, about 12 mm long. Staminodes $\frac{1}{2}$ –1 mm long; rudimentary petals 1–3 mm long. Style nearly glabrous, the stigma semilateral, not capitate. Capsules unknown.

Holotype: *Guédes* PG 1591 in PG. Isotypes in: BM, F, G, P, US. Cotypes: *Ducke* PG 15547 in PG (duplicates: BM, F, G, P, RB, US) and *Ducke* PG 15658 in PG (duplicates: BM, F, US).

Distribution: Amazone basin, mainly in Para.

BRAZIL, Para: Belem, *Ducke* PG 15547, 15658; —, *Guédes* PG 1591; Rio Tapajoz, *Ducke* PG 16427; —, *Capucho* 446; Faro, *Ducke* RB 20566. Matto Grosso: along Madeira-Mamoré railroad, *Kuhlmann* RB 17767. Amazonas: Manaus, *Ducke* RB 23485; —, *Riedel* s.n.; —, *Ferreira* 530.

COLOMBIA, Uaupès: Mitu, *P. H. Allen* 3342.

BRITISH GUIANA: Upper Essequibo river, *Myers* 5662; Berbice-Demarara watershed, *Forest Dept. Brit. Guiana* 832.

PERU, Amazonas: Rio Marañon, near mouth of Santiago, *Tessmann* 4291 sec. *Pilger* l.c.

Ecology: In terra firma forests; fl. Sept.–Febr.

Vernacular names: Para: Lacreiro.

Uses: Wood used for roofs (Para).

Observation: "Delicious scent, somewhat like violets. One of the loveliest flowering trees I ever saw" J.G. Myers in sched.

37. ***Qualea calophylla*** Pittier, Contr. Fl. Ven. (Arb. Arbust. Nuev.) 29. 1923; — *Bol. Soc. Cienc. Nat.* 4(30): 88. 1938; this publication fig. 2b.

Large or medium-sized tree. Branchlets glabrous. Apex of the stipules acute, deciduous, the base persistent, greyish, subglandular, about 2 mm wide, axillary nectaries absent. Petioles 12–20 mm long. Leaf-blades glabrous, firmly coriaceous, oblong or elongate elliptic-oblong, $7-12 \times 3\frac{1}{2}-5$ cm; the apex obtuse-acuminate; the base rounded or subobtus; the midrib narrowly winged below; more than 20 about equally strong lateral nerves per cm (near the midrib); veinlets numerous on almost the entire surface. Inflorescence an ample, many-flowered raceme composed of 1-flowered cincinni. Pedicels densely ferrugineous-tomentose, 12–17 mm long. Flower-buds obtuse, 17–25 mm long. Calyx reddish, the lobes densely ferrugineous-sericeous, rounded, the minor ones about 10–12, 12–15, 14–16 and 15–18 mm respectively, the spurred lobe up to 25 mm long; the spur dependent, puberulous, about 6–8 mm long, obtuse, the base slightly constricted. Petal white with red and yellow streaks, obcordate, about $4\frac{1}{2}$ cm long and wide. Anther pilose on the back, lanceolate-ovate, acute, 8–9 mm long; the filament nearly glabrous, about 12–14 mm long. Staminodes (or rudimentary petals) linear, 1–2 mm long. Style glabrous. Capsules ellipsoid, about 5 cm long, the brownish exocarp minutely tuberculate.

Holotype: *Jahn* 500 in US.

Distribution: Northern Venezuela.

VENEZUELA, Carabobo: *Funk & Schlim* 637. Aragua: *Pittier* 15444, 15720, 14045. Federal District: *Ernst* s.n.; *Jahn* 500, 543, 1335.

Ecology: In lowland and mountain forests not reached by seasonal floods; from the lowlands up to 1500 m; fl. May–Sept.; fr. (one rep.) Jan.

Vernacular names: The name “floreccillo” used by Pittier in 1923 is not really in use for this tree (*Pittier* 1938).

38. ***Qualea magna*** Kuhlmann, An. Prim. Reun. Sul-Am. Bot. 3: 80. 1938.

Large tree. Branchlets pubescent in youth, glabrous in age, the cortex not exfoliating. Stipules about $\frac{1}{2}$ –1 mm long, acute, the base incrassate; extrafloral nectaries above the stipules, urceolar-subglobose, diam. about 1 mm. Petioles slender, subpuberulous, 7–10 mm long. Leaf-blades subcoriaceous, glabrous, oblong, $7-8\frac{1}{2} \times 1\frac{1}{2}-2\frac{1}{2}$ cm; the apex obtuse or obtuse-acuminate; the base subacute; the midrib puberulous, not or narrowly winged; more than 20 about equally strong lateral nerves per cm; veinlets on nearly the entire surface. Panicle loose, rachis and pedicels densely puberulous. Pedicels 10–14 mm long. Flower-buds $15-18 \times 9-12$ mm. Calyx-lobes ciliate and subpuberulous, the first one 8–10 mm diam., the other minor ones 10–13 mm long, the spurred lobe about 18 mm long, the spur enclosed by the lateral lobes, ellipsoid, $6-7 \times 4-5$ mm. Petal white, painted with red above the base, obcordate, emarginate, about $5-5\frac{1}{2}$ cm long and up to 7 cm wide. Stamen glabrous, the anther recurved, ovate-lanceolate, acute, about 8–10 mm long; the filament 13–15 mm long. Staminodes and rudimentary petals present. Style glabrous, about $1\frac{1}{2}$ cm long. Capsules unknown.

Holotype: *Kuhlmann* 196 = RB 34385 in RB. Isotypes in: K, U, US.

Distribution: Espirito Santo.

BRAZIL, Espírito Santo: Corrego de Durao, Linhares, Rio Doce, *Kuhlmann* 196 = RB 34385, 432 = RB 57596.

Ecology: In the zone of the coastal forests; fl. Apr.

Vernacular names: Angelica.

Uses: Lumber tree.

39. ***Qualea schomburgkiana*** Warm. Flora Bras. **13**(2): 39. 1875.

Large or medium-sized tree. Branchlets glabrous. Stipules acute, about 1 mm long, with crateriform about 1 mm wide axillary glands. Petioles 7–17 mm long. Leaf-blades glabrous, firmly coriaceous, oblong or elliptic-oblong, $7-13 \times 3-5\frac{1}{2}$ cm; the apex acute, obtuse or shortly acuminate; the midrib two-winged below; more than 10 major lateral nerves per cm, minor ones in between; veinlets near the margin. Inflorescence composed of racemes bearing 1(–2) flowered cincinni. Pedicels subpuberulous, slender, 10–17 mm long. Flowers fragrant, the buds acute, 17–25 mm long. Calyx reddish, green-tinged, the minor lobes rounded, subsericeous or nearly glabrous, the first one about 10×7 mm, the other ones $12-15 \times 7-9$ mm; the spurred lobe rounded, greyish sericeous outside, up to 25 mm long, ovate-elliptic; the spur dependent, glabrous, straight, $7-10 \times 2-3$ mm; the apex acute, the base constricted. Petal white, streaked with vermilion in the centre, flushed with yellow at the base, obcordate, up to 4×6 cm. Stamen glabrous; the anther recurved, about 6 mm long, subacute; the filament up to 15 mm long. Rudimentary petals (or staminodes) 3–5 mm long. Style glabrous except the basal 1–3 mm; the stigma indistinctly three-lobed. Capsules unknown.

Holotype: *Ri. Schomburgk* 893 in B (photograph in F). This specimen (with Warming's handwriting) is now destroyed; the GH duplicate is proposed as the lectotype. *Ro. Schomburgk* 1047₁ (BM, G, K, L, P, W) cited by Warming in the second place cannot be taken as the lectotype since Warming makes a certain reservation.

Distribution: Roraima district and Pacaraima ridge.

BRITISH GUIANA: Roraima, *Ri. Schomburgk* 893; —, *Ro. Schomburgk* 1047; —, — 584; —, — VII; —, *Forest Dept. Brit. Guiana* 2827; —, *Im Thurn* 79; —, *Tate* 206.

VENEZUELA, Bolivar: Roraima, *Pinkus* 64; Pacaraima, St. Teresita de Kavanayén, *Steyermark* 60490; —, Ptari-tepui, *Steyermark* 60710, 60674; Caroni R., *Cardona* 1704; Cuquenán R., *Ule* 8627.

Ecology: In mountain forests, often along small rivers ("on brooks" *Ro. Schomburgk*), on rocky banks, etc.; fl. Oct.–March.

40. ***Qualea tuberculata*** Stapf. nov. spec. (*fig. 13*).

Subgenus *Qualea*, sectio *Qualea*. Arbor magna. Ramuli glabri, haud decorticantes. Stipulae irregulares, linea haud prominula junctae; basi incrassata et haud decidua; apice acuto et deciduo. Glandulae in axillis stipularum tuberculiformes, poro apicali praeditae, diam. 1–2 mm. Petiolus 14–18 mm longus. Lamina glabra, subcoriacea, oblonga vel elliptico-oblonga, 11–17 cm longa et 4–7 cm lata; apice breviter obtuse-acuminata; basi subrotundata et brevissime attenuata; costa subtus bialata; nervis lateralibus ultra 30 per cm, tenuissimis et creberrimis, inter se venulis transversalibus prope marginem junctis. Inflorescentia ampla, thyrsoides; cincinnis bi- vel rarius unifloris;

pedicellis pubescentibus, 13-18 mm longis. Flores fragrantis. Alabastra 14-18 mm longa. Calycis laciniae pallido-roseae, minores extra subpuberulae, 8-11 mm longae; lacinia major extra dense sericea, circa 18-20 mm longa et lata. Calcar ellipsoideum, circa 4-5 mm longum, sub anthesi calycis lacinia secunda obtectum. Petalum fere album, carinatum, ad 5 cm longum et latum. Stamen glabrum vel fere glabrum; anthera late-elliptica, acuta, circa 8 mm longa et 4 mm lata;

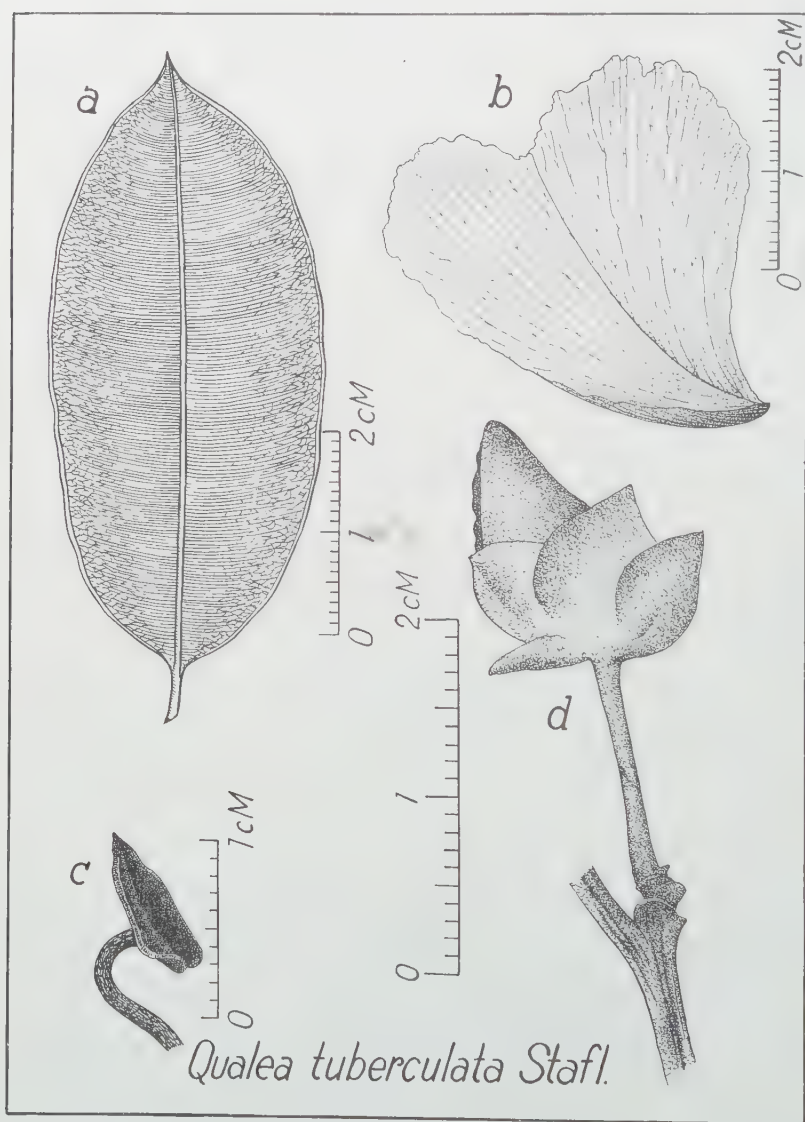


Fig. 13. *Qualea tuberculata* Staf!. a. Leaf; b. petal; c. stamen; d. flower-bud.

filamento crasso ad 15 mm longo. Stylus circa 10 mm longus. Capsula ignota.

Holotype: *Ll. Williams* 14384 in F. Isotype in US.

Distribution: Venezuelan Amazonas.

VENEZUELA, Amazonas: Rio Guainía, *Ll. Williams* 14384, 14830.

Ecology: In high forests on terra firma; fl. Febr.–March; 127 m.

Observation: Characterised by the peculiar (tuberculate) extrafloral nectaries in the axils of the stipules, the large, oblong leaves, the broad-elliptic anther, etc.

41. ***Qualea decorticans*** Ducke, Arch. Inst. Biol. Veg. 4: 39. 1938.

Large tree. Branchlets glabrous, the cortex exfoliating. Stipules minute; axillary glands urceolar with thick walls, 1 mm wide, $\frac{1}{2}$ mm high. Petioles 10–18 mm long. Leaf-blades coriaceous, glabrous, lanceolate, $7\text{--}11 \times 2\frac{1}{2}\text{--}3\frac{1}{2}$ cm; the apex long acute-acuminate (10 mm); the base obtuse or acute; the midrib narrowly two-winged below; more than 40 lateral nerves per cm, hardly prominent; veinlets numerous on the entire surface. Panicle many-flowered, cincinni 1–4 flowered. Bracts triangular. Pedicels puberulous, slender, 5–8 mm long. Flower-buds acute, 13–17 mm long. Calyx in vivo cyaneo-violaceous, the lateral lobes subpuberulous and ciliate, 4–6 mm long, the anterior lobes obtuse, nearly glabrous, 6–8 mm long; the spurred lobe elliptic-oblong, up to 17 mm long; the spur glabrous, subcylindrical, 4–5 mm long. Petal pink, obcordate, emarginate, $2\frac{1}{2}\text{--}3 \times 3\text{--}3\frac{1}{2}$ cm. Anther subacuminate, about 7 mm long, the back pilose; the filament glabrous, somewhat flattened, about 10 mm long. Rudimentary petals and staminodes linear, the former up to 8 mm, the latter about $\frac{1}{2}$ –1 mm long. Ovary subpilose. Style glabrous, about 10 mm long. Capsules unknown.

Holotype: *Ducke* RB 34667 in RB. Isotypes in: G, IAN, K, NY, P, S, U, US.

Distribution: Once collected.

BRAZIL, Amazonas: Cucuhy on the Venezuelan-Brazilian border between the Rio Negro and the granitic mountains, *Ducke* RB 34667.

Ecology: In somewhat swampy forest not reached by seasonal floods; fl. Sept.

42. ***Qualea suprema*** Ducke, Arch. Inst. Biol. Veg. 2: 53. 1935; Ducke 1938 p. 39.

Shrub or small tree. Branchlets glabrous, the cortex not exfoliating. Persistent bases of the stipules subprominent, about 1 mm long. Petioles 4–7 mm long. Leaf-blades glabrous, thinly coriaceous, when dry yellowish-green, lanceolate, lanceolate-ovate or suboblong, $7\text{--}10 \times 2\frac{1}{2}\text{--}3\frac{1}{2}$ cm; the apex gradually long acute-acuminate (10–15 mm); the base obtuse or nearly rounded; the midrib narrowly two-winged below; about 10 main lateral nerves per cm, one minor one in between each pair; veinlets in- or subconspicuous. Inflorescences few-flowered up to 6 cm long racemes composed of 2–3 pairs of 1–2 flowered cincinni. Pedicels slender, 12–20 mm long, subpuberulous or glabrous, slightly incrassate towards the apex. Flower-buds acute, about $2\text{--}2\frac{1}{2}$ cm long, subpuberulous outside. Calyx in vivo dirty violaceous, the minor lobes rounded, up to 16 mm long; the spurred lobe up to $2\frac{1}{2}$ cm

long, obtuse-rounded; the spur ellipsoid, 3–6 mm long, hidden between the other lobes. Petal blue with a yellow base, $4\frac{1}{2}$ –6 cm long and wide, obcordate, emarginate, in vivo laterally involute and curved. Stamen glabrous, the anther 10–12 mm long, slightly recurved, the connective wide, the locules narrow, marginal; the filament somewhat flattened, thick, about 13 mm long. Staminodes linear, 3–4 mm long. Style glabrous, 15–18 mm long. Capsules unknown.

Holotype: *Ducke* RB 24161 in RB. Isotypes in: K, P, S, U, US.

Distribution: Upper Rio Negro region.

BRAZIL, Amazonas: Rio Curicuriary, affl. Rio Negro, *Ducke* RB 24161, 336 = RB 34662; Rio Ia affl. Marié, *Froes* 22389.

Ecology: In lowland forests, flooded by seasonal floods (varzea); fl. Nov.–June.

43. ***Qualea cyanea*** *Ducke*, Arch. Inst. Biol. Veg. 2: 54. 1935 p. 54; *Ducke* 1938 p. 38.

Large tree. Branchlets glabrous, the cortex not exfoliating. Stipular glands subprominent, about 1 mm wide. Petioles 12–15 mm long. Leaf-blades coriaceous, glabrous, elliptic-oblong or ovate-elliptic, $7\text{--}11 \times 4\frac{1}{2}\text{--}6$ cm; the apex abruptly and shortly obtuse-acuminate; the base obtuse, both often folded; the midrib not winged; 10–15 major subprominent lateral nerves per cm, one minor one in between each pair; veinlets in- or subconspicuous. Panicle terminal, loose, often surpassing 20×20 cm, composed of racemes bearing several pairs of 1(–2) flowered cincinni. Pedicels subpuberulous, slender, 8–15 mm long. Flower-buds 13–16 mm long. Calyx in vivo dark violaceous, whitish puberulous outside, the first lobe about 7–8 mm, the other minor ones about 10–11 mm long; the spurred lobe broadly elliptic, emarginate, 16–20 mm long; the spur cylindrical, about 6 mm long, covered by the second lobe. Petal blue with a yellow central streak, obcordate, emarginate or two-lobed, about $30\text{--}35 \times 35\text{--}42$ mm. Anther pilose on the back, lanceolate, apiculate, about 5 mm long; the filament glabrous. Staminodes, if present, linear, about 1 mm long. Style nearly glabrous, 7–12 mm long. Capsules unknown.

Holotype: *Ducke* RB 24165 in BR. Isotypes: IAN, K, NY, P, S, U, US.

Distribution: Once collected.

BRAZIL, Amazonas: between Jacurapá and Puruité rivers (affl. Rio Ica), *Ducke* RB 24165.

Ecology: In moist places in terra firma forest; fl. Oct.

Section C. ***Costatifolium*** *Staf.* nov. sect.

Series II. *Costatae* Warm. Flora Bras. 13(2): 32. 1875 (latin diagn.).

Trees or shrubs. Buds mostly perulate. Stipules represented by subprominent, crateriform glands with a dark interior and a thick, callous, lighter coloured margin. Leaves pilose or glabrous, nearly equal-sided; midrib impressed above, strongly prominent below; major lateral nerves less than 8 per cm, subparallel, making an angle of $60\text{--}80^\circ$ with the midrib; anastomosing veinlets distinct and numerous; marginal nerve undulate. Flower-buds ovoid, the minor lobes not closely adpressed against the spurred lobe. Stamen glabrous, the anther

dorsifixed, distinctly shorter than the filament. Staminodes rarely present. Ovary densely hirsute, abruptly merging into the slender style. Stigma subcapitate.

Type-species: *Qualea grandiflora* Mart.

Distribution: Three species in the region of the campos and four in the Hylaea.

Key to the species

- 1a. Cortex of the branchlets not exfoliating (or rarely with small fragments). Spur shorter than 10 mm 2
- b. Cortex of the branchlets exfoliating. Spur 15–25 mm long in adult flowers 44. **Q. grandiflora** Mart.
- 2a. Leaves distinctly pilose below 3
- b. Leaves glabrous below; on young ones sometimes some scattered hairs 5
- 3a. Petal mainly blue. Flower-buds 5–7 mm long, about as long as the spur 4
- b. Petal mainly white. Flower-buds about 10 mm long, the spur distinctly shorter, densely lanuginose with patent hairs 45. **Q. multiflora** Mart. ssp. **pubescens** (Mart.) Stafl.
- 4a. Apex of the leaves obtuse, sometimes subacute or rounded. Spur straight or slightly curved 46. **Q. parviflora** Mart.
- b. Apex of the leaves acuminate. Spur strongly incurved towards the pedicel 47. **Q. dinizii** Ducke
- 5a. Lateral nerves at 1–5(–6) mm distance 6
- b. Lateral nerves at 7–15 mm distance 11
- 6a. Petal mainly white. Flower-buds longer than 9 mm; the spur shorter than the bud 7
- b. Petal mainly blue. Flower-buds 5–7 mm long, about as long as the spur 8
- 7a. Spur glabrous; 4–7 major lateral nerves per cm. see no. 31. **Q. gracilior** Pilger
- b. Spur densely pilose; 1–3 main lateral nerves per cm. 45. **Q. multiflora** Mart. ssp. **multiflora**
- 8a. Spur patent, curved, about as long as the bud 9
- b. Spur stretched along the back of the fourth calyx-lobe, somewhat longer than the bud 48. **Q. tessmannii** Mildbr.
- 9a. Apex of the leaves acuminate 10
- b. Apex of the leaves mostly obtuse, sometimes subacute or rounded 46. **Q. parviflora** Mart.
- 10a. Base of the leaves rounded and narrowly cordate. Spur incurved towards the anterior lobes and sometimes touching them 49. **Q. rupicola** Ducke
- b. Base of the leaves, in particular of the young ones, acute or obtuse, never cordate. Spur incurved towards the pedicel 47. **Q. dinizii** Ducke
- 11a. Base of the leaves rounded or cordate. Inflorescence a terminal raceme of 2–3 flowered epedunculate cincinni : 12

- b. Base of the leaves gradually narrowing towards the petiole, the extreme base narrowly cordate. Inflorescence a panicle of regular, peduncled, three-flowered cymes see no. 51. **Q. cymulosa** Schery
- 12a. Perulate buds conical, acuminate, about 4 mm long. Capsules 3–4 cm long 50. **Q. psidiifolia** Spruce ex Warm.
- b. Perulate buds ovoid, subacute, 1–2 mm long. Capsules 8–9 cm long see no. 58. **Q. megalocarpa** Staffl.

41. **Qualea grandiflora** Mart. Nov. Gen. Sp. 1: 133. *t.* 79. 1824; Schult. 1827 p. 102; Spreng. 1827 p. 10; DC. 1828 p. 29; A. Dietr. 1831 p. 99; Don 1832 p. 671; D. Dietr. 1839 p. 21; Ettingshausen 1861 p. 185; Warm. 1867 p. 29; — 1875 p. 41 *t.* 8 *II*; — 1889 p. 22; — 1892 p. 224; Wille 1882 p. 181 seq. (anat.); Malme 1900 p. 44; — 1905 p. 7; — 1924 *t.* I fig. 2; Chodat 1902 p. 736; Chodat & Hassler 1903 p. 243; Glaziov 1905 p. 30; L. B. Smith 1945 p. 300; Macbride 1950 p. 877; Hoehne 1951 p. 257. *Qualea ecalcarata* Mart. 1824 p. 131. *t.* 78; Schult. 1827 p. 101; Spreng. 1827 p. 10; DC. 1828 p. 29; A. Dietr. 1831 p. 99; Don 1832 p. 671; Reichenbach 1836 *t.* 332 (fide Warm. 1875 p. 42); D. Dietr. 1839 p. 21; Warm. 1875 p. 42. *Schuechia brasiliensis* Endl. ex Walp. 1843 p. 68, 1845–46 p. 663. *Schuechia ecalcarata* Warm. 1867 p. 33.

Tree, the trunk often distorted; the young branchlets, buds, petioles, midrib and lower surface of the leaves tomentellous; the cortex of the branchlets exfoliating. Perulate buds ovoid. Crateriform bases of the stipules 1–2 mm long; the tops wanting or minute and then acute. 0–4 Accessory glands sometimes present. Petioles 6–10 mm long. Leaf-blades coriaceous, discolor, oblong, or suboblong, 10–20 × 4–8 cm; the apex shortly acuminate; the base rounded, subcordate or obtuse; 30–45 main lateral nerves on either side at about 3–7 mm distance. Cincinni 1–4 (mostly 2-) flowered, arranged in terminal or axillary racemes; cincinni sometimes axillary. Rachis, peduncles, pedicels and bracts tomentellous. Bracts obtuse, 6–9 mm long. Peduncles up to 5 mm long. Pedicels 10–20 mm long. Flower-buds about 15–25 mm long. Flowers fragrant. Calyx sericeous outside; the lobes rounded or obtuse; the spur cylindrical, up to 30 mm long, elegantly curved. Petal white with a yellow base or yellow, obcordate-orbicular, up to 4 × 6 cm. Anther about 10 mm long with a triangular, more or less V-shaped connective and narrow, marginal locules; the apex subacute, the base cordate, adhering to the about 15 mm long filament somewhat above the base. Staminodes 2, about 1 mm long. Style glabrous. Capsules about 6–8 cm long, ovoid; the base rounded; the apex apiculate; glabrous, dull and minutely verruculose outside; the exocarp woody, 4–6 mm thick, the endocarp about 1 mm thick. Seeds numerous, the wings about 4 mm long.

Holotype: *Martius* s.n. in M (Sao Paulo, in the fields near Ypanema). Holotype of *Q. ecalcarata* Mart., of *Schuechia brasiliensis* Endl. ex Walp. and of *Schuechia ecalcarata* Warm.: *Martius* s.n. in M (Minas Geraes) Note: *Q. ecalcarata* is the type-species of the genus *Schuechia* Endl. (1836–40 p. 1178).

Distribution: In the Central Brazilian Campos and the Amazonian Campinas. BRAZIL. Paraná: Itararé, *Dusen* 3541, 9655, 11237, 16138. São Paulo: Ypanema, *Martius* s.n., 114; *Rignell* III 527; *Vagas* 5548; *Mosen* 1270, 1271; *Hennenderf* 264, 269; *Löffgren* 1089. Minas Geraes: Numerous collections in many herbaria, e.g. *Martius* s.n.; *Glaziou* nos. 17611, 17612, 9794, 14696, 19154. Goyaz: *Gardner* 3143; *Pohl* 428; *Lutzelburg* 437; *Ule* 326; *Glaziou* 20633, *Brade* 15472; *Burchell* 6106, 8255. Bahia: *Blanchet* 3081; *Lutzelburg* 3098, 3099. Ceará: *Löffgren* 288. Piahy: *Dalgren* 871; *Gardner* 2162; *Lutzelburg* 14074. Maranhão: *Carolina*, *Pires & Black* 2005; 2222. Vitória, *Pires & Black* 1693a. Matto Grosso: *Lindmann* A 2729; *Malme* I 1142; *Moore* 740; *Robert* 570b. Para: *Spruce* s.n. 336; *Kuhlmann* RB 17769; *Ducke* PG 3585 = RB 14068, PG 8159; *Da Costa* 299. Amazonas: Rio Madeira, *Krukoff* 5821A.

PARAGUAY: Rio Apa, *Fiebrig* 4465, *Hassler* 7881, 7881a; Sa de Maracayú, *Hassler* 5583; Co Noaga, *Anisits* 2024, 2365, 2837.

BOLIVIA: Santa Cruz, Sara, Buenavista, *Steinbach* 6785; Velasco, *Kuntze* s.n.; Imapassa, *R. S. Williams* 528; Atten, *R. S. Williams* 1575.

Ecology: Characteristic tree of the "campos cerrados", mostly with distorted trunks (cf. orchard trees). Protected against fires and drought by an extremely thick, suberous cortex. Outside the campo-region found in similar vegetations (savannas, campinas, etc.). The tree bears flowers during the rainy season: in Central Brazil especially in Nov., Dec. and Jan. but occasionally from Oct.-March (Fr.: Febr.-April; new leaves: Aug.-Oct.), in lower Amazonia from Febr.-June. After fire sometimes flowering in the dry season (*Malme* 1905 l.c.).

Vernacular names: BRAZIL: Pao terra, Páu terra, Páu terra uassú, Páu terra do campo, Páu terra da folha larga (grande); regional names: Minas Geraes: Páu santo, Arvore de terra, Uva puva do Campo; Para: Ariuaú.

Observation 1: It is possible that *Agardhia grandiflora* Spreng. (1827 p.17) and *Lozania grandiflora* Schult. (1827 p. 109) are also later synonyms for this species, but this cannot be established with any certainty. Sprengel mentions no type and his description does not cover completely that of *Q. grandiflora*. Schultes cites *Agardhia grandiflora* as a synonym to his *Lozania grandiflora*, but not to *Q. grandiflora* or *Q. ecalcarata*.

Observation 2: *Q. ecalcarata* Mart. differs from this species only by the absence of the spur and the occasional occurrence of two stamens and two petals. The one collection is apparently a monstrosity.

Observation 3: *Glaziou* (1905 p. 30, ex Taub.) refers the specimen *Glaziou* 17611 (in P) to a non-described variety. The relevant specimen has somewhat shorter and wider leaves but this variation does not seem to justify the description of a separate variety.

45. **Qualea multiflora** Mart. Nov. Gen. Sp. 1: 134. t. 80. 1824; Spreng. 1827 p. 9; Schult. 1827 p. 100; DC. 1828 p. 29; A. Dietr. 1831 p. 100; Don 1832 p. 671; D. Dietr. 1839 p. 21; Ettingshausen 1861 t. 80; Warm. 1867 p. 30; — 1875 p. 44 t. VII; Wille 1882 p. 181 seq. (anat.); Petersen 1896 p. 318; Malme 1900 p. 45; Glaziou 1905 p. 30; Correa 1931 p. 263 (vern. names, uses).

ssp. **multiflora** (includes: var. *glabra* Mart. l.c., Schult. l.c.; D. Dietr. l.c.).

Small tree or shrub, the trunk often distorted, the vegetative parts glabrous; the cortex of the branchlets not exfoliating. Perulate buds ovoid, 3–4 × 1–2 mm. Stipular glands 1–2 mm wide, often some smaller accessory glands on the internodes. Leaves mostly opposite, rarely in trimerous whorls or nearly scattered. Petioles 2–5 mm long. Leaf-blades coriaceous, often oblong or broadly lanceolate, sometimes also ovate or elliptic, 7–16 × 2–7 cm; the apex short-acuminate, sometimes obtuse or acute; the base obtuse or rounded, sometimes

subcordate; 15–25 major lateral nerves on either side, prominent below, minor ones in between, disappearing in the reticulate venation. Upper part of the inflorescence a raceme of 2–5 flowered cincinni, the lower part branched with the cincinni on the branches. Bracts acute or acuminate, 3–5 mm long. Peduncles 1–5 mm long. Pedicels 5–10 mm long, puberulous with mixed longer and shorter hairs. Flower-buds obtuse, about 10 mm long. Flowers fragrant. Calyx densely fulvous sericeous, the lobes rounded, the spur subclavate or cylindrical, rounded, straight in youth but curved in age, 5–8 mm long, the lanuginose indumentum composed of mixed longer and shorter hairs contrasting with the sericeous indumentum of the lobes. Petal obcordate, two-lobed, white or later yellow, spotted with red or violet, up to 3×3 cm. Stamen 10–14 mm long, the anther recurved and subacute, the connective incrassate, adhering to the slender filament somewhat above the cordate base. Style slender, glabrous except the basal 1–2 mm. Capsules up to 3 cm long, the exocarp minutely verruculose, brownish, woody, about 2 mm thick.

Holotype: *Martius* s.n., Minas Geraes (“in campis raro arboribus obsitis”) in M.

Distribution: Central Brazilian Plateau and Northern Paraguay.

BRAZIL, Minas Geraes: *Martius* s.n.; *Glaziou* 17613; *Claussen* div. coll.; *Lund* s.n.; *Warming* s.n.; *Reinhardt* s.n.; *Pohl* 5848; *Regnell* III 528c, — II 99; *Oliveira* s.n.; *Barreto* 7134, 7135, 7138; *St. Hilaire* B² 2359, C² 294. Sao Paulo: *Hemmendorf* 268, 286; *Mosen* 1272, 1273, 1274; *Löfgren & Edwall* 13537; *Burchell* 5214; *Gaudichaud* 857, *Lund* s.n. Parana: *Dusen* 16506, 11724. Matto Grosso: *Regnell* III 526x; *Kuntze* s.n. Rio de Janeiro: Nova Friburgo, *Glaziou* 19148.

PARAGUAY: Sierra de Amanbay, *Hassler* 10734, 10738.

Ecology: In campo-vegetation on dry grounds or in semi-deserts; fl.: wet season, mainly Nov.–March, occasionally later; fr.: Febr.–Aug. The leaves fall in the last months of the dry season (July–Sept.); the new leaves appear in the first months of the wet season.

Vernacular names: BRAZIL, Minas Geraes & Sao Paulo: Uva puva do Campo, Páu terra; Rio de Janeiro: Louro-tinga. Correa (l.c.) cites: Páu terra do campo, Páu de Tucano, Cinzeiro.

Use: The wood is used for canoes and as lumber (Correa l.c.).

ssp. **pubescens** (Mart.) Staf. nov. comb. *Q. multiflora* Mart. var. *pubescens* Mart. 1824 p. 135 (latin diagnosis); Schult. 1827 p. 100; DC. 1828 p. 29; Don 1832 p. 671; D. Dietr. 1839 p. 21. *Qualea jundiahy* Warm. 1867 p. 31 fig. 5, 6; — 1875 p. 45 t. VII fig. 1; Wille 1882 p. 181 seq. (anat.); Petersen 1896 p. 318 fig. 172A; Malme 1900 p. 46; Löfgren 1903 fig. 32 fide Index Londinensis; Glaziou 1905 p. 30; Kuhlmann & Kühn 1947 p. 81, 162. *Qualea pilosa* Warm. 1875 p. 45; — 1889 p. 23; Wille 1882 p. 181 seq. (anat.); Malme 1900 p. 45; Pilger 1901 p. 166, 230; Chodat & Hassler 1903 p. 243; Glaziou l.c.; Malme 1905 p. 8; Hoehne 1914 p. 52 t. 10; Erdtman 1952 p. 452. *Qualea virgata* Rusby 1912 p. 99.

Differs from the ssp. *multiflora* by the presence of a whitish-greyish, often brownish indumentum on the lower surface of the leaves, on the branchlets, the petioles and the perulate buds.

Lectotype: *Martius* s.n. in M. Martius does not indicate a particular specimen. It can be assumed that he used his own collections from Minas Geraes and Sao Paulo. The sheets in the Munich herbarium bear blank labels and one of these

has been chosen as the type. Holotype of *Q. jundiahy* Warm.: Warming s.n. at Lagoa Santa, in C. Holotype of *Q. pilosa* Warm.: Regnell III 528 (29-11-1849 or 1848) in S. Only one of the numerous Regnell III 528 sheets bears the indication *Q. pilosa* in Warming's handwriting. Branchlets from what appears to be the same tree on other sheets are named *Q. jundiahy*. Holotype of *Q. virgata* Rusby: R. S. Williams 415 in NY, duplicates in BM, K, US.

Distribution: Central Brazilian Plateau, Eastern Bolivia and Northern Paraguay.

BRAZIL, Minas Geraes: Regnell III 528b, III 1760; Mexia 5581, 5641; Pohl 2860; Warming s.n. (Lagoa Santa); Glaziov 19150a; Barreto 8514; St. Hilaire B² 2352, 2353, s.n.; Weddell 2847; Claussen div. coll. Sao Paulo: Regnell III 528a; Mosen 4144; Hemmendorf 216; Riedel 459. Rio de Janeiro: Glaziov 3956, 19148. Goyaz: Gardner 3146; Pohl 3930; St. Hilaire C¹ 731, 732, 902bis; Glaziov 20684; Ule 325. Matto Grosso: Malme I 1168; Robert 643; Gaudichaud 305. Piahy: Gardner 3144. Bahia: herb. Kegel 12340. Maranhao: Pires & Black 2478.

BOLIVIA: Velasco, Kuntze s.n.; Imapaza, R. S. Williams 415, 397; Ixiamos, Cardenas 2002.

PARAGUAY: Upper Apa river, Hassler 8144.

Ecology: In campo vegetation ("cerrado", "capoes de mata", "mata aberta" and "capueira") up to 1000 m. Characteristic cerrado tree: much-branched and the distorted trunk and branches provided with a thick cortex (cf. *Q. grandiflora*, *Vochysia cinnamomea*). Fl.: wet season, mainly Nov.-March, occasionally later. Fr.: April (one report). Flowers visited by several insects, e.g. by common bees (Kuhlmann & Kühn l.c.).

Vernacular names: BRAZIL, Minas Geraes: Páu terra, Páu terra da folha miuda, Páu terra do mato; Jundiahy (at Lagoa Santa).

Observation 1: Warming (1875) describes two separate species (*Q. pilosa* and *Q. jundiahy*). In the opinion of the present author these two species cannot stand, in particular when the greatly enlarged number of specimens and the subsequent wider knowledge of the variability of this group is taken into account. The differences are (cf. Warming l.c.): a. *Q. jundiahy* has a less developed indumentum than *Q. pilosa*, the limb of the leaves being usually visible between the hairs; b. the petioles differ in length; c. the calyx-lobes differ in structure. The arguments b. and c. have to be dropped at once; the enlarged material shows a variability in these respects excluding specific differences. The first point is of some importance, but in this respect too a series of intermediate forms is found (cf. Claussen 489 in S) and it is often impossible to decide whether a specimen belongs to *Q. jundiahy* or to *Q. pilosa*. It would be impracticable to distinguish even varieties. In the present treatment both species of Warming are described under the ssp. *pubescens* of *Q. multiflora*. The differences of the "multiflora" group on the one hand and the "pubescens" group on the other, are not of a specific character. The flowers, the nervation and the shape of the leaves, the stipules and the glands are always alike and the only difference can be found in the indumentum. Martius describes a var. *pubescens* "a que ceterum nullo modo differt". The rank of subspecies seems more appropriate since both groups differ in an — admittedly small — group of characters and because of the absence of intermediate forms.

Observation 2: *Qualea virgata* Rusby differs in no respects from the present species. No differences are mentioned by Rusby himself!

Observation 3: *Qualea macroptera* A. Dietr. (1831 p. 101) and *Qualea subvillosa* Link ex A. Dietr. (1831 p. 101) may also belong to this species. The descriptions of A. Dietrich are, however, inadequate; no types were mentioned. The Berlin collections which could have given further information are now destroyed. The description of both species, although rather short, does not contradict our supposition. A Sellow specimen "ex Berlin" is preserved in US; it bears the annotation *Q. macroptera* Lk. and belongs clearly to this subspecies.

Qualea subvillosa Link ex A. Dietr. var. *glabrifolia* A. Dietr. is possibly identical with the ssp. *multiflora*.

46. ***Qualea parviflora*** Mart. Nov. Gen. Sp. 1: 135. t. 81. 1824; Spreng. 1827 p. 10; Schult. 1827 p. 103; DC. 1828 p. 29; A. Dietr.

1831 p. 100; Don 1832 p. 671; D. Dietr. 1839 p. 21; Schnizlein 1843-70 *t.* 260 fig. 2, 6-15; Ettingshausen 1861 *t.* 80; Warm. 1867 p. 30; — 1875 p. 43; — 1889 p. 22; Wille 1882 p. 181 seq. (anat.); Malme 1900 p. 45; — 1924 *t.* 1, 3; Pilger 1901 p. 165, 230; Chodat 1902 p. 736; Chodat & Hassler 1903 p. 243; Glaziov 1905 p. 30; Ducke 1938 p. 41; Standley 1933 p. 20; Hoehne 1951 p. 257. *Qualea parviflora* Mart. var. *tomentosa*, var. *glabrata* & var. *discolor* Mart. l.c. (also Schult., DC., Don and D. Dietr. l.c.).

Small tree or shrub with distorted trunk and branches and with a thick, suberous cortex. Branchlets often puberulous in youth, the cortex not exfoliating. Stipular glands about 1 mm long; often some accessory glands scattered on the internode. Petioles 3-6 mm long. Leaf-blades coriaceous, in general oblong, 5-14 × 1½-4 cm, extremely variable in size, shape and indumentum, glabrous or tomentellous; the apex obtuse, subacute, rounded or emarginate, often mucronulate; the base obtuse or rounded. Lateral nerves slender, subprominent below, the major ones often at 2-4 mm distance with minor ones and a reticulate venation in between. Inflorescences cylindrical. Racemes terminal and axillary, cylindrical, up to 20 × 4 cm, composed of 2-6 flowered epedunculate cincinni, the latter sometimes congested and the flowers in semi-whorls. Pedicels pubescent, slender, 5-15 mm long. Flower-buds obtuse, about 6-7 mm long. Calyx greyish-whitish sericeous outside, the spurred lobe more or less convolute; the spur cylindrical or subclavate, 6-8 mm long, straight or slightly curved. Petal violaceous or coeruleous, the base whitish and subpilose, about 1½-2 cm long and 2 cm wide. Anther about ½ mm long, the connective incrassate with marginal locules, often strongly recurved; the filament about 5 mm long. Staminodes and rudimentary petal sometimes present. Style about 5 mm long. Capsule up to 3½ cm long, ovoid-oblongoid, the woody, resinous exocarp about 1 mm thick, verruculose.

Lectotype: *Martius* s.n. (Minas Geraes ad Arraial das Contendas) in M. Martius does not cite a precise locality. Of the several Munich specimens the one with a complete label, belonging to the "var. *tomentosa*" has been chosen as the lectotype. The specimen depicted on *t.* 81 (Mart. 1824) was composed for the occasion.

Distribution: Widely distributed in Southern and Central Brazil, Eastern Bolivia and Northern Paraguay.

BRAZIL, Minas Geraes: Numerous collections in many herbaria. Sao Paulo: Regnell III 526; Hemmendorf 265. *Martius* s.n. Goyaz: Gardner 3145; Burchell 6108, 6008, 7280, 8520, 7591; St. Hilaire C¹ 800; Machado 435; Siek B 24. Matto Grosso: Malme I 1036, II 1806, II 2291; Lindmann A 3031; Moore 486; Robert 568, 568b. Ceara: Duarte 1491; Dahlgren 882; Miranda 7; Löfgren 635, 320; Gardner 1597; Lützelburg 12492, 25880, 16171, 26206. Maranhao: Ducke 2183; Froes 11712, 21577, 24248; Pires & Black 2309, 2579, 2166. Piauh: Lisboa PG 2397. Bahia: Blanchet 2808; Lützelburg 2094, 3024; Zehntner 402. Para: Capucho 488; Da Costa 224. Amazonas: Ducke RB 34663.

BOLIVIA: Tipuani-Guanai, Bang 1663; O. Velasco, Kuntze s.n.; Yungas, Weddell 4214.

PARAGUAY: Sierra de Maracayù, Hassler 5590; Upper Apa river, Hassler 8229; Sierra de Amanbay, Hassler (*Rojas*) 10692; Apa river, Anisits 2424; —, Fiebrig 4013 (4964).

Ecology: In campo vegetation, mainly on dry and stony ground. The leaves fall at the end of the dry season (July-Sept.); the flowers appear shortly after the

first rains (Sept.–Dec.). Malme (1905 l.c.) states that the flowers may appear before the rains after fire. Fr. Apr.–Sept. Characteristic tree of the campos cerrados with *Q. multiflora*, *Q. grandiflora* and *Vochysia cinnamomea*.

Vernacular names: BRAZIL, Ceara: Craiba. Minas Geraes: Páu terra, Páu terra con folhas miudas, Páu terra do campo, Páu terra miuda. Maranhao: Páu de Judeu, Judeu.

Use: The wood is used as timber.

47. **Qualea dinizii** Ducke, Arch. Jard. Bot. Rio 1: 49. t. 17, 19E. 1915; — 1938 p. 41; Pfeiffer 1926 p. 354; A. C. Smith 1939 p. 188; Mennega 1948 p. 46; Stafleu 1951 p. 195. *Qualea dinizii* Ducke var. *glabrifolia* Meurs ex Amshoff 1948 p. 12 (nomen nudum).

Large tree. Branchlets subpuberulous or glabrous, the cortex exfoliating (small fragments). Perulate buds ovate, acute, pilose. Stipular glands subprominent, less than 1 mm wide. Petioles 2–4 mm long. Leaf-blades subcoriaceous, generally oblong, up to $11 \times 4\frac{1}{2}$ cm but on flower-bearing branchlets usually much smaller; the apex acuminate; the base acute in youth; glabrous above, puberulous and glabrescent below; lateral nerves straight, 3–5 major ones per cm with minor ones in between, subprominent above, not so below; major veinlets subprominent above, the minor ones inconspicuous above and distinctly reticulate below. Racemes whitish-pubescent, mainly axillary, up to 10 cm long, composed of 1–2 flowered cincinni. Peduncles $\frac{1}{2}$ –1 mm long. Pedicels slender, 4–6 mm long. Flower-buds about 5 mm long, whitish-sericeous pubescent. Minor calyx-lobes 2–3 mm long; the spurred lobe carinate, about 4–5 mm long; the spur cylindrical, 4–6 mm long, strongly curved. Petal lilac or violaceous, obcordate, emarginate, $10\text{--}13 \times 13\text{--}18$ mm. Anther about 1 mm long with a thick connective and semicircularly curved locules. Staminalodes absent. Style glabrous, about 3 mm long. Capsule up to 5 cm long, oblongoid, the apex obtuse, the exocarp dull, rugulose, woody, about 3 mm thick.

Holotype: *Ducke* PG 7991 in PG. Isotypes in: BM, G. Cotypes: *Ducke* PG 9028, 11261, 15006, 15641.

Distribution: Eastern Hylaea.

BRAZIL, Para: Rio Mapuera, *Ducke* PG 9028; Rio Tocantins, *Ducke* PG 15641; Lower Rio Trombetas, *Ducke* PG 15897; Obidos, *Ducke* RB 13695; Rio Trombetas, Castanhas do Rio Cuminá, *Ducke* PG 7991; Ariramba, *Ducke* PG 11261; Rio Erepecurú, *Ducke* PG 15006. Amazonas: Terr. Rio Branco, *Froes* 23034.

BRITISH GUIANA: Kanuku Mts., A. C. Smith 3250.

SURINAME: (Full details cf. Stafleu 1951 p. 196) Sectie O: *B. W.* nos 2394, 2814 3811, 4173, 4320, 4914, *Boschbeheer* 53, *Woodherb.* 59, 59a. Zanderij I: *B. W.* nos. 738, 1501; Wia Wia bank, *Lanjouw & Lindeman* 1195.

Ecology: In forests on high grounds. Fl.: towards the end of the dry season (Oct.–Dec.). Fr. March (one rep.).

Vernacular names: BRAZIL, Para: Quaruba, Páu mulato da Terra Firme. SURINAME: (cf. Stafleu l.c.) e.g.: Wassie-wassie-kwarrie (Negro-English).

Observation: Named to honour José P. Diniz, organizer of the expedition on which Ducke discovered this species (*Ducke* 1915 p. 50).

48. **Qualea tessmannii** Mildbr. Notizbl. Berlin 9: 141. 1924; Macbride 1950 p. 879.

Tree of medium size. Branchlets in youth puberulous with long and

short hairs, the cortex not exfoliating; in age glabrous, densely lenticellate. Stipular glands subprominent, about 1 mm wide. Perulate buds slender, about 2 mm long. Petioles 2–3 mm long. Leaf-blades coriaceous, glabrous except the midrib, oblong-lanceolate, 40–70 × 12–19 mm; the apex obtuse or sometimes obtuse-acuminate; the base obtuse; the lateral nerves slightly curved, at 1–2 mm; veinlets reticulate. Inflorescence a terminal 6–10 cm long raceme composed of 1–4 flowered epedunculate cincinni, some of the latter in the axils of the upper leaves. Rachis provided with many short and some longer hairs. Pedicels slender, 2–5 mm long, puberulous. Flower-buds 5–7 mm long. Calyx greyish-sericeous outside; the spurred lobe about 6 mm long, conically involute; the spur rounded, subclavate, pilose, stretched along the back of the lobe, about 6–7 mm long. Petal violet, cuneate-suborbicular, the base pilose, 10–12 mm long and wide. Anther about 1 mm long, the locules semicircularly curved; the filament about 5 mm long, narrowed towards the anther. Staminodes not present. Style 4 mm long, glabrous. Capsule 2½–3 cm long, the exocarp woody, resinous, squamulose, about 1 mm thick.

Lectotype: *Tessmann* 3451 in S. The holotype (*Tessmann* 3451 in B) was destroyed during world war II. Photograph of the B specimen in F.

Distribution: Peru and Northern Bolivia.

PERU, San Martín: Juanjui, *Klug* 4275. Loreto: Middle Ucayali, *Tessmann* 3451.

BOLIVIA, La Paz: San Yungas, basin of Rio Bopi, *Krukoff* 10124.

Ecology: In forests outside reach of seasonal floods. Up to 900 m. Fl. Dec.; fr. July.

49. ***Qualea rupicola*** Ducke, Arch. Inst. Biol. Veg. 4: 41. 1938.

Small tree with distorted trunk and reddish cortex. Branchlets subpuberulous in youth, glabrous and densely lenticellate in age, the cortex not exfoliating. Stipular glands about 1 mm wide. Petioles 2–5 mm long. Leaf-blades thinly coriaceous, glabrous, oblong or ovate-elliptic, 5–9 × 2–4 cm; the apex subabruptly obtuse-acuminate (top about 10 mm long); the base rounded and narrowly cordate, often folded; main lateral nerves thin, subprominent, at 2–4 mm distance; veinlets reticulate, subprominent. Raceme terminal, densiflorous, composed of 2–3 flowered, epedunculate cincinni, 8–12(–18) cm long, densely greyish-pubescent on all parts. Bracts 2–4 mm long. Pedicels 2–5 mm long. Flower-buds 5–6 mm long; the spur exerted already in young buds. Calyx densely greyish-sericeous outside; the minor lobes rounded, 3–5 mm long; the spurred lobe 5–6 mm long, subcarinate, often convolute; the spur strongly incurved, often curved around the pedicel towards the back of the third lobe, 5–6 mm long. Petal violaceous, up to 15 × 18 mm, obcordate, emarginate, the base pilose. Anther with small connective and semicircularly curved narrow locules; the filament 5–7 mm long. Staminodes not present. Style glabrous, 5–6 mm long. Capsule up to 28 mm long.

Holotype: *Ducke* RB 34674 in RB. Isotypes in: G, IAN, K, P, S, U, US. Distribution: Once collected.

BRAZIL, Amazonas: Rio Negro, Serra do Jacamim, above St. Isabel, *Ducke* RB 34674.

Ecology: On rocks on top of granitic mountains; fl. March.

50. ***Qualea psidiifolia*** Spruce ex Warm. *Flora Bras.* **13**(2): 46. *t.8 fig. 1.* 1875; *Ducke* 1938 p. 42.

Large tree. Branchlets glabrous or pilose with about 1 mm long hairs, the cortex not exfoliating. Perulate buds conspicuous, conical, about 4 mm long, the outer scales acuminate. Stipular glands about $1-1\frac{1}{2}$ mm long. Petioles 5–10 mm long, subpilose. Leaf-blades thinly coriaceous, glabrous except the midrib below, oblong or elliptic-oblong, up to 18×6 cm; the apex shortly obtuse-acuminate; the base rounded or cordate, sometimes folded; the major lateral nerves at irregular distances, 8–15 on either side, not prominent above, prominent below, ending in the undulate marginal nerve at about 3–6 mm from the margin, a smallish secondary marginal nerve close to the margin; veinlets reticulate, subprominent. Raceme terminal, up to 10 cm long, composed of 2–3 flowered cincinni, fulvous-villose, the hairs up to 2 mm long. Bracts 4–5 mm long. Peduncles 0–3 mm long. Pedicels 8–15 mm long. Flower-buds 8–10 mm long, adpressed villose outside. Spuried calyx-lobe conically convolute, 7–9 mm long; the spur about as long as or somewhat longer than the lobe, clavate, recurved, patent. Petal pink, obcordate, about $2\frac{1}{2} \times 2\frac{1}{2}$ cm. Anther about 2×1 mm, the locules recurved, the filament about 7 mm long. Staminodes not present. Style glabrous, 7–9 mm long. Capsule about 3(–4) cm long, squamulose-verruculose, the valves elliptic-oblong; the apex obtuse; the exocarp woody, about $1\frac{1}{2}$ mm thick.

Holotype: *Spruce* 3059 in C. Isotypes in: BR, G, GOET, K, NY, OXF, P, RB, U, W. ("near San Carlos"). Cotype: *Spruce* 3059 (fr.) ("ad flumina Cassiquiari, Vasiva et Pacimoni").

Distribution: Upper Rio Negro Region.

BRAZIL, Amazonas: Along Cassiquiari, Vasiva and Pacimoni rivers, *Spruce* 3059 (fr.); Cucuhy, Upper Rio Negro, *Ducke* RB 34664; Rio Curicuriary, affl. Rio Negro, *Ducke* RB 23791.

VENEZUELA, Amazonas: San Carlos on Rio Negro, *Spruce* 3059 (fl.).

Ecology: In riverine forest; fl. Sept.–Oct.

Section D. **Polytrias** Staffl. nov. sect.

Arbor, ramulis hornotinis ad basim perulis instructis, gemmis perulatis, foliis basi subobliquis, nervis lateralibus haud numerosis (5–8), subparallelis, sub angulo circa 60–80' e costa ortis. Axes inflorescentiarum secundarii cymas pedunculatas regulariter trichotomas formant. Petalum basi pilosum. Stamen glabrum, anthera dorsifixia filamento brevior, connectivo subincrassato. Petala rudimentaria vel (et) staminodia absunt. Ovarium dense hirsutum, abrupte in stylum transiens.

Type-species: *Qualea cymulosa* Schery.

Distribution: One species in Panama and adjacent Colombia.

Observation: The name refers to the numerous three-flowered cymes in the inflorescence.

51. ***Qualea cymulosa*** Schery, Ann. Missouri Bot. Gard. **36** 3): 285. 1949.

Large tree. Branchlets puberulous in youth, glabrous and densely lenticellate in age. Stipular glands crateriform, the margin light-brownish; a small accessory gland 1–3 mm below the main ones. Petioles 5–9 mm long. Leaf-blades elliptic or obovate-elliptic, up to 13×6 cm; the apex acute-acuminate; glabrous except the midrib and the axils of the lateral nerves below; major lateral nerves 5–8 on either side; marginal nerve at about 3–4 mm from the margin, often rather incomplete; minor lateral nerves and veinlets reticulate. Inflorescence terminal or axillary; the peduncles 12–14 mm long, the pedicels 8–10 mm long. Flowers “showy, rose-pink”. Flower-buds about 7 mm long. Calyx densely greyish-sericeous outside; the spurred lobe conically convolute, about 7 mm long; the spur bag-shaped, rounded, constricted near the base, about 4 mm long. Petal obcordate, two-lobed, up to $2 \times 2\frac{1}{2}$ cm, the base pilose below. Anther nearly 2 mm long, recurved, the connective subincrassate; the filament about 5 mm long. Style glabrous except the base. Fruit about 5 cm long; the valves oblong; the base and apex obtuse; the exocarp minutely verruculose outside, about 3 mm thick; the endocarp thin, its three parts connate at the base after dehiscence of the fruit.

Holotype: *P. H. Allen* 4645 in MO. Isotypes in K, U.

Distribution: Panama and adjacent Colombia.

PANAMA, Darien: Headwaters of Rio Chico, *P. H. Allen* 4645.

COLOMBIA, Bolivar: Lands of Loba, *Curran* 169.

Ecology: Up to 600 m.; fl. June; fr. Apr.–May.

Observation: The peduncled three-flowered cymes are not found in any other species of *Qualea*. The species is allied to those of the section *Costatifolium* by the convolute spurred calyx-lobe, the structure of the stamen, the nervation of the leaves, etc. Apart from being morphologically isolated *Q. cymulosa* is also geographically isolated: it is the only Central American species of the genus.

Subgenus II: **AMPHILOCHIA** (Mart.) Staf. nov. comb.

Amphilochia (genus) Mart. Nov. Gen. Sp. **1**: 127. 1824 (latin diagnosis); Spreng. 1827 p. 4, — 1830 p. 21; DC 1828 p. 26; A. Dietr. 1831 p. 96; Don 1832 p. 669; Meisn. 1836–43 **1**: 119, **2**: 85; Endl. 1836–40 p. 1177; D. Dietr. 1839 p. 21. *Qualea* series *Amphilochia* Warm. 1875 p. 32.

Trees or shrubs. Cortex of the branchlets not exfoliating. Cataphylls deciduous, crowded near the base of the branchlets. Perulate buds in the axils of both cataphylls and ordinary leaves. Leaf-bases often oblique. Lateral nerves subparallel, rather few, the central ones making an angle of about 60–80° with the midrib, curved upwards, ending in the margin, anastomosing or ending in a strongly undulate marginal nerve at some distance from the margin. Cincinni epedunculate, mostly opposite, thick-set. Minor calyx-lobes not closely adpressed against the fourth lobe, the latter not provided with a spur but sometimes somewhat hollow or gibbous at the base. Petal firm, subchartaceous (at least the unguiculate base) but the margins often membranous, densely pilose on both sides. Anther distinctly shorter

than the filament, the connective not incrassate, the locules linear, adhering to the filament somewhat above the base of the back. Staminodes not present. Ovary densely hirsute, abruptly merging into the style, the base of the latter hirsute (except *Q. glaziovii*). Exocarp of the capsules woody, blackish, squamulose-verruculose, mostly partly releasing from the thin endocarp.

Type-species: *Qualea dichotoma* (Mart.) Warm. (*Amphilochia dichotoma* Mart.).

Distribution: Eight species widely distributed in the Extra Amazonian Province of Brazil and in adjacent parts of Bolivia and Northern Paraguay.

Observation: Named after Amphilochos, the post-Aristotelian writer on forage-plants (cited by Plinius).

Key to the species

- 1a. Branchlets and lower surface of the leaves pilose. 2
- b. Branchlets and leaves glabrous. 5
- 2a. Perulate buds subglobose, apically rounded, the outer scales closely adpressed 3
- b. Perulate buds elongate-ovoid, apically acuminate, the outer scales divergent 52. **Q. lundii** Warm.
- 3a. Leaf-bases rounded and mostly cordate. Nervation subprominent below 4
- b. Leaf-bases acute or obtuse, sometimes subrotundate, never cordate. Nervation strongly prominent below 53. **Q. selloi** Warm. ssp. **pubescens** Staff.
- 4a. Petioles 5–10 mm long, leaves 5–8 × 3–4 cm 54. **Q. dichotoma** (Mart.) Warm. var. **dichotoma**
- b. Petioles 10–15 mm long, leaves 5–12 × 3–6 cm 54. **Q. dichotoma** (Mart.) Warm. var. **elongata** (Warm.) Staff.
- 5a. Leaf-blades firmly coriaceous. Petioles firm (1–3 mm thick), relatively short: length less than 1/7 th of that of the leaf-blade 9
- b. Leaf-blades thinly coriaceous. Petioles slender (less than 1 mm thick), relatively long: length 1/4–1/6th of the length of the leaf 7
- 6a. Leaf-bases cordate, wide 7
- b. Leaf-bases acute or obtuse, sometimes somewhat rounded, never cordate 53. **Q. selloi** Warm. ssp. **selloi**
- 7a. Leaves 3–8 × 1½–4½ cm (on flowering branchlets), if larger: nervation subprominent below 8
- b. Leaves 9–15 × 5½–8½ cm (on flowering branchlets), the nervation strongly prominent below 55. **Q. densiflora** Warm.
- 8a. Inflorescence loose: the flowers of adjoining pairs of cincinni not touching each other 56. **Q. cordata** Spreng. var. **cordata**
- b. Inflorescence dense-flowered; the flowers of adjoining pairs of cincinni touching each other. Leaves acute or subacute 56. **Q. cordata** Spreng. var. **intermedia** (Warm.) Staff.

- 9a. Leaf-blades $1\frac{1}{2}$ –2 times longer than wide, apically shortly acute-acuminate, acute, obtuse or rounded 10
 b. Leaf-blades $2\frac{1}{2}$ –3 times longer than wide, apically gradually acute-acuminate 57. **Q. glaziovii** Warm.
 10a. Capsules less than 3 cm long. Petioles 8–16 mm long 11
 b. Capsules 8–9 cm long. Petioles 6–10 mm long 58. **Q. megalocarpa** Stapf.
 11a. Leaf-blades generally ovate, apically acute or obtuse 59. **Q. cryptantha** (Spreng.) Warm. var. **cryptantha**
 b. Leaf-blades generally oblong, apically rounded or obtuse 59. **Q. cryptantha** (Spreng.) Warm. var. **marginata** (Miq.) Stapf.

52. **Qualea lundii** (Warm.) Warm. Flora Bras. **13**(2): 47. t. 9. 1875; Warm. 1889 p. 23; Wille 1882 p. 181 seq. (anat.); Petersen 1896 p. 318 fig. 172 K, L; Glaziov 1905 p. 30. *Amphilochia lundii* Warm. 1867 p. 27, 45 fig. 10.

Shrub or small tree. Branchlets subpuberulous. Perulate buds elongate-ovoid, acuminate, subpuberulous, 3–6 mm long, the outer scales divergent. Stipular glands concave, hardly prominent, about 1 mm long. Petioles 3–14 mm long. Leaf-blades firmly coriaceous, obovate, oblong or elliptic, $5\text{--}9 \times 2\frac{1}{2}\text{--}5$ cm, nearly glabrous above, densely adpressed tomentellous below; the apex often more or less rounded; the base often cuneate; the nervation impressed above and prominent below, 8–15 lateral nerves on either side, anastomosing or ending in a marginal nerve exactly along the margin; the veinlets numerous, conspicuously reticulate. Flowers in 6–12 flowered pseudo-whorls along a rachis and in the axils of the leaves. Bracts about 1 mm long. Pedicels about 1–2 mm long. Flower-buds about 8–10 mm long. Calyx adpressed subpubescent, the lateral lobes about 3 mm, the anterior ones 6–7 mm long; the fourth lobe $8\text{--}10 \times 10\text{--}12$ mm. Petal broadly elliptic, about 10 mm long, densely sericeous on both sides, slightly fleshy. Stamen glabrous; the anther oblong, apiculate, about 4 mm long. Capsule $2\text{--}2\frac{1}{2}$ cm long, the valves oblong, the apex acute, the woody exocarp $\frac{1}{2}\text{--}1$ mm thick.

Holotype: *Warming* s.n. (Serra da Piedade, 3-2-1866) in C.

Distribution: Minas Geraes.

BRAZIL, Minas Geraes: Serra da Piedade, *Warming* s.n. (3-2-1866); Caraça, Glaziov 14697.

Ecology: In campo cerrado vegetation and along fringe of forests; up to 1300 m; fl. Dec.–Febr.; fr. Febr. (one rep.).

Observation: The “dichotomy” in this and other species of the subg. *Amphilochia* is a false one caused by an obliteration at a late date of the top of a branchlet. No dichotomy is observed in Glaziov’s well developed specimen.

53. **Qualea selloi** Warm. Flora Bras. **13**(2): 49. 1875; Wille 1882 p. 181 seq. (anat.).

ssp. **selloi**

Tree. Branchlets and leaves glabrous or nearly so. Older branchlets lenticellate. Perulate buds subglobose, glabrous, the outer scales

closely adpressed. Stipular glands subprominent, about 1 mm long; minor accessory ones often situated below the major ones. Petioles 14–18 mm long. Leaf-blades firmly coriaceous, elongate-elliptic, broadly lanceolate, oblanceolate or suboblong, $10\text{--}13 \times 4\text{--}5$ cm; the apex acute or shortly acute-acuminate, often oblique; the base acute, obtuse or nearly rounded; 9–14 lateral nerves on either side, not parallel (the angles with the midrib between 30 and 70°), irregularly curved, prominent below, real marginal nerve absent; major veinlets prominent below, minor ones not so. Raceme composed of 2–3 flowered cincinni, one or two pairs of cincinni in the axils of the upper leaves. Pedicels pilose, 2–4 mm long. Flower-buds 8–10 mm long. Minor calyx-lobes subsericeous outside, 5–8 mm long; the fourth lobe about 10 mm long. Petal membranous, densely pilose, especially in the centre, purplish and spotted with red and yellow (Hoehne). Anther glabrous, about 3 mm long; the filament slender, whitish pilose. Style about 10 mm long. Capsules about $2\frac{1}{2}$ cm long; the exocarp about 1 mm thick; valves oblong, the apex apiculate.

Lectotype: *Sellow* 346 in US. Isotypes in: BR, G, NY, P, U. The *Warming* holotype was preserved in Berlin (cf. photograph in F); this specimen was destroyed during world-war II and the US duplicate has been chosen as the lectotype. None of the known isotypes bears Warming's handwriting.

Distribution: Once collected.

BRAZIL, Sao Paulo: *Sellow* 346; cult. Jard. Bot. Sao Paulo, *Hoehne* 28397.

Ecology: The cultivated specimen: fl. et fr. Oct.

ssp. **pubescens** Staffl. nov. ssp.

Petoli et folia subtus dense pubescentes. Ramuli, gemmae perulatae et rachis pubescentes. Petioli 10–18 mm longi.

Holotype: *Claussen* s.n. in W (coll. Reichenbach 124203), isotypes in W (id. 124223) and US.

Distribution: Mainly in Minas Geraes.

BRAZIL, Minas Geraes: *Claussen* s.n., 219A, 42(119), 338, 430(1430); 439A, 441, 133A, 134A (numbers different in different herbaria). Sao Paulo: *St. Hilaire* C¹ 1193.

Observation: The *Claussen* specimens have hitherto been named *Q. glauca* Warm. This species, however, is based on specimens (*Pohl* s.n., *Netto* s.n., *Claussen* 484) that differ greatly from the above-mentioned ones. The shape, structure and dimensions of the leaves bring the *Claussen* specimens to *Q. selloi*; they differ from the type specimen (and the type-subspecies) by the presence of an indumentum on all parts.

54. **Qualea dichotoma** (Mart.) Warm. *Flora Bras.* 13(2): 48. 1875; Wille 1882 p. 181seq. (anat.); Correa 1931 p. 116. *Amphilochia dichotoma* Mart. 1824 p. 128 t. 177; Spreng. 1827 p. 10; Schult. 1827 p. 106; DC. 1828 p. 26; A. Dietr. 1831 p. 96; Don 1832 p. 669; D. Dietr. 1839 p. 21

var. **dichotoma**

Shrub or small tree. Young parts of the branchlets, petioles, lower surface of the leaves, rachis, and pedicels densely pubescent. Branchlets often pseudo-dichotomous. Stipular glands inconspicuous, $\frac{1}{2}$ –1 mm long. Perulate buds subovoid, about $1\text{--}1\frac{1}{2}$ mm long, the scales ad-

pressed. Petioles 5–10 mm long. Leaf-blades coriaceous, oblong, oblong-ovate or elliptic-oblong, $5-8 \times 3-4$ cm; the apex mostly rounded or subobtuse; the base rounded or cordate; lateral nerves 8–15 on either side, subprominent below, major veins subprominent below, minor ones not so; marginal nerve not present. Inflorescence cylindrical, dense-flowered, up to 12 cm long, the flowers in clusters composed of pairs of 1–3 flowered cincinni. Pedicels about 2 mm long. Bracts 2–4 mm long. Flower-buds about 8–10 mm long. Minor calyx-lobes subsericeous outside, the lateral ones about 4–5 mm, the anterior ones about 5–7 mm long; the fourth lobe sericeous on the back of the base, about 8–10 mm long. Petal yellow or whitish, spotted with purple, about 10 mm long, sericeous on all parts but densest on the back, the base thickish. Anther nearly glabrous, 3–4 mm long, apically obtuse; the filament subpilose on the base, 5–8 mm long. Style 6–8 mm long. Capsules $2-2\frac{1}{2}$ cm long, the exocarp about 1 mm thick; the valves oblong-elliptic; the apex acute or obtuse.

Lectotype: *Martius* s.n. in M. The *Martius* specimens in Munich bear no labels mentioning localities. Some confusion exists but there is no reason to doubt that the sheets were indeed used by *Martius*. The one specimen with flowers and a fruit has been chosen as the lectotype.

Distribution: Southern Brazil.

BRAZIL, Minas Geraes: Barra do Jiquitibeo, *Riedel* s.n.; —, *Langsdorff* 822; Sierra do Callony, *Barreto* 12133 (*F. Markgraf* 3313); Diamantina, *Barreto* 9309; *Martius* s.n.; *Gardner* 4554. Goyaz: *Pohl* s.n. Espirito Santo: *Lützelburg* 7219.

Ecology: In campo vegetation; fl. Sept.–Nov.; fr. Nov. (one rep.).

Vernacular names: Cascudo (fide *Correa* l.c.). This name is applied also to two *Cenostigma* (*Caesalp.*) species with leaves like those of *Q. dichotoma*.

var. **elongata** (Warm.) Staff. nov. comb. *Qualea elongata* Warm. *Flora Bras.* 13(2): 48. 1875; *Kuhlmann & Kühn* 1947 p. 81. *Qualea glauca* Warm. l.c. p. 49 t. 10; Warm. 1889 p. 23; *Petersen* 1896 p. 318 fig. 172B; *Glaziou* 1905 p. 31; *Malme* 1905 p. 8; *Kuhlmann & Kühn* 1947 p. 81.

Shrub or tree. Petioles 10–14 mm long. Leaves $5-12 \times 3-6$ cm, the nervation prominent or strongly prominent on the lower surface; the upper surface often distinctly glaucous.

Holotype: *Riedel* s.n. (Curvelho, Minas Geraes) in C. Isotypes: G, GH, K, NY, P, S, US, W. Type material of *Q. glauca* see obs. below.

Distribution: Southern Brazil.

BRAZIL, Rio de Janeiro: Nova Friburgo, *Glaziou* 12664; —, *Claussen* s.n. Minas Geraes: *Claussen* 484; Arcos, *Oliveira* 163; Curvelho, *Riedel* s.n.; Morada, *Netto* s.n.; Carandai, *Duarte* 690. São Paulo: Cotia, *Constantino* 152 = RB 45514. Goyaz: Fazenda do Rajadinho, *Glaziou* 20685; Upper Tocantins river, *Ule* 69. Mato Grosso: Santa Anna da Chapada, *Malme* II 2380, 2380a.

Ecology: In the thickets and the open forests of the campo vegetation, rarely in the open campo cerrado itself or on stony ground. Up to 1300 m. Fl. Sept.–Nov.; fr. Febr., Apr. (two rep.).

Vernacular names: Goyaz: Cascudo. Minas: Carvalho brasileiro (Carvalho = Oak).

Use: "The timber is of a good quality, hard and heavy" (*Duarte* in sched.).

Observation: *Warming* (1875 l.c.) makes a distinction between *Q. dichotoma*, *Q. elongata* and *Q. glauca* but adds in a note that the future may demonstrate these species to be one and the same. In 1889 he mentions *Glaziou* 12664 as an inter-

mediary form between *Q. glauca* and *Q. elongata*. The differences between the latter species cannot stand: a number of specimens has now come to hand showing a gradual variation from subprominent to sharp-prominent lateral nerves, the length of the petioles varies from 10 to 14 mm (Warming: *Q. glauca* 12–13 mm, *Q. elongata* 10–12 mm). The indumentum too is not fundamentally different: Warming states: “molliter pubescentia” in *Q. elongata* and “patenter pilosa” in *Q. glauca*. This is only a gradual developmental difference. The present author cannot detect a specific or even a varietal difference between these forms.

The difference between the vars. *elongata* and *dichotoma* is found mainly in the length of the petioles and the size of the leaves. In all other respects these forms are exactly alike.

It should be noted that of the specimens listed by Warming under *Q. glauca* the *Pohl* (s.n.) specimen belongs to the var. *dichotoma* (short petioles) whereas the *Netto* (s.n.) and *Claussen* (484) specimens belong to the var. *elongata*. The latter specimen is in agreement with Warming's description and chosen as the lectotype of *Q. glauca*. For this reason *Q. glauca* is cited (in this treatment) under var. *elongata*.

55. ***Qualea densiflora*** Warm. Flora Bras. 13(2): 50. 1875; Malme 1900 p. 47; Glaziou 1905 p. 31.

Tree. Branchlets and leaves glabrous. Perulate buds subglobose, 1–2 mm wide, the scales closely adpressed. Stipular glands subprominent, 1–1½ mm long, the margin light-coloured; sometimes two or three accessory glands below the major one. Petioles firm, thicker than 1 mm, 1–2 cm long. Leaf-blades firmly coriaceous, ovate, subelliptic or subobovate, somewhat glaucous on both sides, 9–15 × 5½–8½ cm; the nervation not prominent above, distinctly and strongly so below; major lateral nerves 10–14 on either side, curved upwards and disappearing near the margin; major veinlets transversal, minor ones reticulate; marginal nerve not present. Inflorescence dense-flowered, up to 10 × 2 cm, the cincinni in a pseudo-spike, 2–3 flowered, the adjoining pairs often touching each other. Pedicels pubescent, 2–4 mm long. Flower-buds about 8–10 mm long. Calyx-lobes, in particular the inner three, sericeous outside, the fourth lobe oblong, 10–13 × 6–8 mm. Petal whitish-yellowish, densely pilose, especially on the back, deeply emarginate, 12–15 mm long. Anther glabrous, 3–4 mm long; the filament pilose on the base, about 6 mm long. Style 5–7 mm long. Capsule 2–3 cm long, apically acute; the exocarp 1–1½ mm thick, not releasing from the endocarp.

Holotype: *Widgren* s.n. (Minas Geraes) in C. Isotypes in: BR, GOET, GH, K, M, P, S, U, US. Cotypes: *Pohl* s.n. (Paracatu) and *Regnell* III 529.

Distribution: Minas Geraes and Sao Paulo.

BRAZIL, Minas Geraes: Villa do Paracatu, *Pohl* s.n. (or 575?); Caldas and Canna Verde, *Regnell* III 529 (527); *Widgren* s.n. Sao Paulo: Bocaina, *Glaziou* 12664a; Serra de Caracol, *Mosen* 4143

Ecology: In campo vegetation on dry grounds, one report from a forest. Fl. Oct.–Dec. Fr. March (one rep.).

56. ***Qualea cordata*** Spreng. Syst. 1: 17. 1825; Warm. 1875. p. 51; — 1889 p. 23; Wille 1882 p. 181 seq. (anat.); Malme 1900 p. 47; Chodat 1902 p. 736; Glaziou 1905 p. 31; Correa 1931 p. 520. *Amphilochia cordata* Mart. 1824 p. 129; Schult. 1827 p. 107; Spreng. 1827 p. 10; DC. 1828 p. 26; A. Dietr. 1831 p. 97; Don 1832 p. 669; D. Dietr. 1839 p. 21; Warm. 1867 p. 26. *Qualea cordata* Spreng. forma *rupestris* Hassler 1903 p. 244.

var. **cordata**

Small tree. Branchlets and leaves glabrous. Perulate buds subglobose, the outer scales closely adpressed. Stipular glands subprominent, about $\frac{1}{2}$ mm long. Petioles 3–6 mm long, $1\frac{1}{2}$ – $2\frac{1}{2}$ mm wide. Leaf-blades coriaceous, somewhat glaucous, variable in size and shape, ovate, oblong or elliptic-oblong, $4\text{--}9 \times 2\text{--}5$ cm; the apex acute or obtuse, the base cordate; the nervation not prominent above, subprominent below; lateral nerves 8–14 on either side, marginal nerve absent. Inflorescence few-flowered, up to 10×2 cm; the pairs of 1–3(–4) flowered cincinni remote. Pedicels pubescent, 2–4 mm long. Flower-buds 8–10 mm long. Lateral calyx-lobes 5–7 mm long, nearly glabrous; anterior lobes sericeous on the back, $7\text{--}10 \times 5\text{--}6$ mm; the fourth lobe oblong, about 12 mm long, the back sericeous. Petal yellow or whitish, spotted with violet in the centre, about 15–18 mm long, emarginate, membranous except the incrassate base, sericeous in the centre. Anther glabrous, about 5 mm long; the filament slightly pilose, narrowing towards the anther, 6–8 mm long. Capsules $2\text{--}2\frac{1}{2}$ cm long, minutely verruculose, the valves oblong, apically acuminate.

Lectotype: *Sellow* s.n. in P. Sprengel's holotype was *Sellow* s.n. (or 2015) in B (photograph in F). The Berlin specimen is no more extant. Holotype of the forma *ruprestis* Hassler: Hassler 6705 in G.

Distribution: Southern Brazil and Northern Paraguay.

BRAZIL, Minas Geraes: Pohl 2577, 3460, s.n.; Glaziou 12663, 14695, 19149; Sampaio 6843; Vauthier 429; St. Hilaire B¹ 1979; Lund s.n.; Barreto 7149, 7151, 7152, 9245; Duarte 2252, 2751; Warming s.n.; Regnell III 529x; Widgren s.n. Sao Paulo: *Sellow* s.n. (2015); Weir 385; St. Hilaire C¹ 1244; Burchell 4278; Vecchi 408; Campanema RB 14061. Parana: Dusen 10466a, 11725, 10559, 16507, 11748, 11649; Reiss 62, 63; Jönsson (Dusen) 387a; Weir s.n.

PARAGUAY (Northern and Central): Fiebrig 517, 5147, 6363; Hassler 3528, 3528a, 6705, 8790, 12356; Balansa 2014, 2014a; Lindmann I A 3861; Anisits 2363, 2708; Jørgensen 3730.

Ecology: In campo vegetation, often in the "campo cerrado" on stony ground. Fl.: rainy season, mainly Nov.–Jan., but reports from Sept.–June; fr. mainly Jan.–Apr.

Vernacular names: BRAZIL: Dedaleira preta, Páu terra. PARAGUAY: Quebracho falso, Burro-caá.

Use: (Correa l.c.) The wood is used as timber and lumber. The fruits and the bark yield a dye.

Observation 1: The publication by Sprengel (1825) seems to be antedated by that of Martius (1824) but Martius cites Sprengel with precise mention of page and volume!

Observation 2: The forma *ruprestis* Hassler is represented by the specimens Hassler 6705 and Jørgensen 3730. They differ by their fruticose habit, the smaller leaves ($3\text{--}5 \times 1\frac{1}{2}\text{--}2$ cm) and the stronger glaucescence. However, the variation of Hassler 6705 reaches inside the variation of the other specimens. It seems unnecessary to describe different forms when these may be found on one and the same plant.

var. **intermedia** (Warm.) Staff. nov. comb. *Qualea intermedia* Warm. Flora Bras. 13(2): 50. t. 9. 1875.

Leaves ovate or ovate-elliptic, rarely ovate-oblong, the base cordate, the apex acute or shortly acuminate, $6\text{--}9 \times 3\text{--}4\frac{1}{2}$ cm. Inflorescence as in *Q. densiflora*, i.e.: the cincinni arranged in a terminal, densiflorous and multiflorous pseudo-spike (up to 10×2 cm) in which the pairs

of cincinni touch each other; young inflorescences closed cylinders, at least in the upper halves; some cincinni in the axils of the upper leaves.

Lectotype: *Sellow* s.n. in US (from Sao Paulo). Warming's holotype was *Sellow* s.n. in B (now destroyed). The US specimen is well preserved and bears Warming's handwriting.

Distribution: Southern Brazil.

BRAZIL, Sao Paulo: *Sellow* s.n. (5252); *Löfgren* 380. Minas Geraes: Serra de Mutuca, *L. O. Williams* 5439. Bahia: Serra do Sincorá, *Ule* 7316.

Ecology: In campo vegetation; fl. Nov.-Febr.; fr.: Febr. (one rep.).

Observation: The only essential difference between these specimens and those of the var. *cordata* is found in the structure of the inflorescence.

var. **grandifolia** Warm. Flora Bras. **13**(2): 52. 1875.

Branchlets firmer than in var. *cordata*. Petioles about 5 mm long. Leaf-blades up to 12×7 cm. Some cincinni in the axils of the upper three or four pairs of leaves, a few others arranged in a terminal raceme. Petal white, painted with red. (fide Warm. l.c.).

Holotype: Riedel s.n. in LE from Serra de Caraça, Minas Geraes, Brazil, fl. Sept.

Observation: The present author did not see the relevant specimen and has no opinion on its status.

57. **Qualea glaziovii** Warm. Flora Bras. **13**(2): 53. *t. 6 fig. 2*. 1875; Warm. 1889 p. 23; Poulsen 1876 p. 273, — 1881 p. 123; Wille 1882 p. 181 seq. (anat.); Glaziou 1905 p. 31.

Tree. Branchlets and leaves glabrous. Perulate buds ovoid-conical. Stipules in youth triangular, about $\frac{1}{2}$ mm long, in age inflated, the apex breaking away and the limb developing into a thin-walled nectary. Subprominent, discoid, $\frac{1}{2}$ -1 mm long nectaries with a callous margin sometimes found in the axils of the stipules. Petioles slender, 10-15 mm long. Leaf-blades coriaceous, elongate-ovate or -elliptic, $6-11 \times 2-4$ cm; the apex gradually acute-acuminate; the base obtuse or subrotundate, often oblique; the nervation subprominent on both sides; lateral nerves 10-20 on either side, curved upwards near the margin; marginal nerve not present. Inflorescence terminal, short, few-flowered, some 2-3 flowered cincinni in the axils of the leaves, other 1-2 flowered ones in a raceme. Pedicels puberulous, 2-3 mm long. Flower-buds 8-10 mm long. Calyx-lobes subsericeous, the lateral ones 5-7 mm, the anterior ones 6-8 mm, the fourth one 9-11 mm long. Petal white, spotted with purple, about $1\frac{1}{2}$ cm long and wide, the centre hirsute on both sides. Anther glabrous, about 4 mm long; the filament slightly pilose, narrowing towards the anther, about 6-7 mm long. Capsules about $3\frac{1}{2}$ cm long; the exocarp 1(-2) mm thick.

Lectotype: *Glaziou* 2567 in C. Isotypes in BR, K, P. Warming mentions several *Glaziou* specimens in numerical order. The best one is *Glaziou* 2567. Co-types: *Glaziou* 2113 (fr.), 2926, 3957.

Distribution: Rio de Janeiro, in the mountains around the town.

BRAZIL, Rio de Janeiro: Tijuca forest, *Glaziou* 2567, 2113, 2926, 3957, 6473; Alto Macahé, *Glaziou* 16766, 19147. Hort. Bot. Rio de Janeiro, cult. *Ducke*, RB 18372.

Ecology: In mountain forest; fl. Febr.–March, fr. Nov. (one rep.).

Observation: To be distinguished from *Q. cryptantha* by the slender, acute-acuminate leaves with obtuse or subrotundate base and the larger capsules (about $3\frac{1}{2}$ cm long) with a thick exocarp.

58. ***Qualea megalocarpa*** Stapf. nov. spec. (fig. 14).

Arbor media. Ramuli glabri, haud decorticantes. Gemmae perulatae ovoideae, subpuberulae, 1–2 mm longae, perulis exterioribus subacutis. Glandulae subprominentes, ellipticae vel suborbiculares, circa $\frac{1}{2}$ –1 mm longae. Petiolus tenuis, 6–8 mm longus, circa 1 mm latus. Lamina fere glabra, tenuiter coriacea, oblonga vel oblongo-obovata, $6-8\frac{1}{2} \times 3-4$ cm, apice breviter et subabrupte obtuse-acuminata, basi rotundata, nervis in utraque pagina haud prominentibus, nervis lateralibus subparallelis, haud numerosis (intervallum 4–7 cm), nervo limbali margini parallelo junctis; venulis numerosis, reticulatis. Inflorescentia terminalis. Flores ignoti. Capsula magna (circa 8–9 cm longa) in pedunculo crasso circa 10–12 mm longo, valvis elongato-ellipticis, circa $2\frac{1}{2}$ cm latis, apice subacuta; exocarpio lignoso, minute verruculoso, extra nigro, 2–4 mm crasso, ab endocarpio tenui haud soluto. Semina ala exclusa elliptica, circa $1-1\frac{1}{2}$ cm longa, ala circa $2\frac{1}{2}-3$ cm longa.

Holotype: *Barreto* 1705 in F.

Distribution: Once collected.

BRAZIL, Minas Geraes: Fazenda do Cachocira, Tobos, *Barreto* 1705 (fr.).

Ecology: In forest; fr. June.

Vernacular names: Merindiba bagre.

Observation: The subgenus to which the species belongs cannot be established with any certainty as long as the flowers remain unknown. The characters of the leaves, which have very much in common with those of *Q. cryptantha*, the glands and the perulate buds make it plausible that the species belongs to the subgenus *Amphilochia*.

59. ***Qualea cryptantha*** (Spreng.) Warm. Flora Bras. **13** 2): 53. t. 12. 1875; Glaziov 1905 p. 31. *Agardhia cryptantha* Spreng. 1820 p. 462; — 1825 p. 17; DC. 1828 p. 30; A. Dietr. 1831 p. 97; Don 1832 p. 672. *Amphilochia cryptantha* Warm. 1867 p. 27. *Amphilochia acuminatula* Gardn. 1843 p. 343; Walp. 1843 p. 915.

var. ***cryptantha***

Tree. Branchlets and leaves glabrous. Perulate buds ovoid or subglobose, 1–2 mm long. Stipules in youth triangular, about $\frac{1}{2}$ –1 mm long, acute, in age inflated, the apex falling off and the limb constituting a thin-walled nectary. Subprominent, discoid, $\frac{1}{2}$ –1 mm long nectaries with callous margin sometimes found in the axils of the stipules. Petioles slender, 8–16 mm long, less than 1 mm thick. Leaf-blades thinly coriaceous, generally ovate, $5-8 \times 3-5$ cm; the apex shortly acute-acuminate, acute or obtuse, rarely subrotundate; the base broadly rounded or subtruncate, often oblique; the nervation hardly prominent; 8–15 main lateral nerves on either side, curved upwards and anastomosing near the margin; marginal nerve absent. Inflorescence terminal, cylindrical, up to 9×2 cm. Cincinni opposite,

2-3(-5) flowered, the pairs remote, the lower ones in the axils of the upper leaves; sometimes all cincinni axillary. Pedicels 2-4(-5) mm long, puberulous. Flower-buds 7-10 mm long. Calyx-lobes sericeous outside, the lateral ones 4-6 mm, the anterior ones 6-8 mm, the fourth lobe 10-12 mm long. Petal $1\frac{1}{2}$ cm long and wide, the centre densely pilose on both sides. Anther glabrous, about 3 mm long, recurved; the

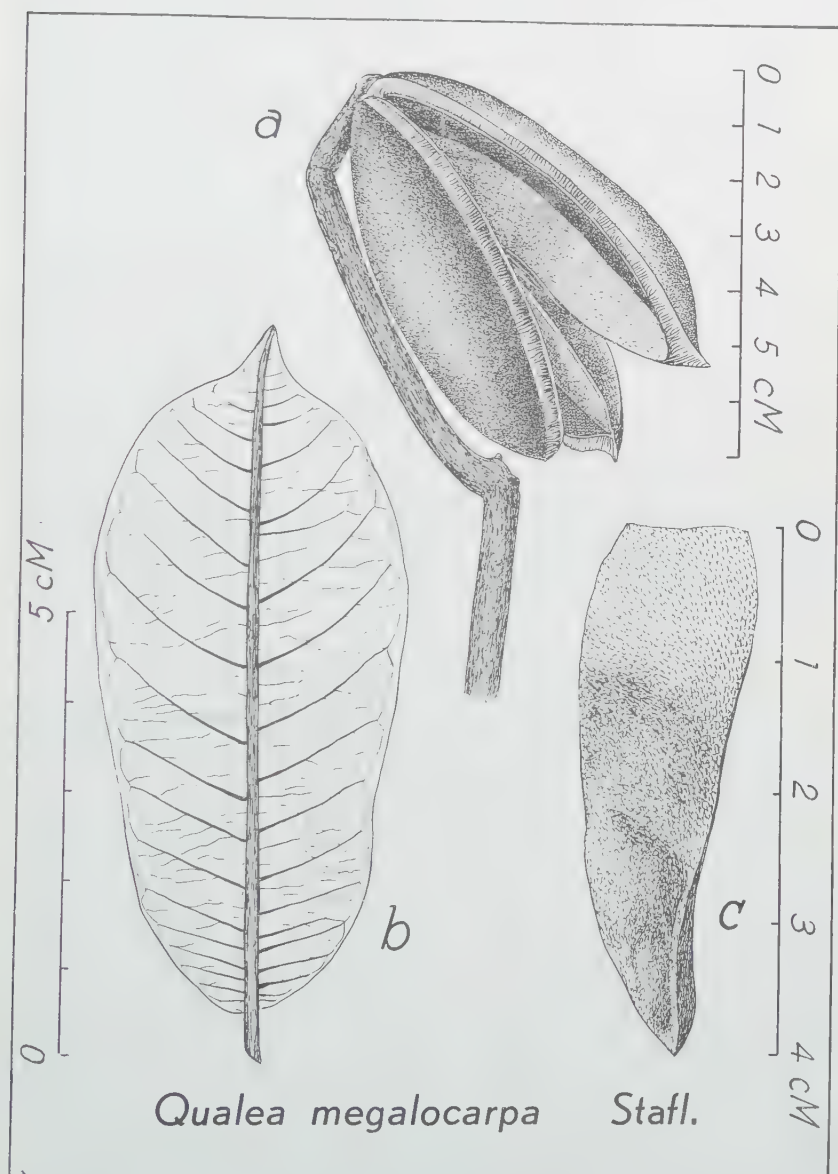


Fig. 14. *Qualea megalocarpa* Stafl. a. Fruit; b. leaf; c. seed.

filament pilose, in particular the base, narrowed towards the anther, about 7 mm long. Capsules 2–2½ cm long, the exocarp less than 1 mm thick, verruculose, not or hardly releasing from the endocarp.

Lectotype: *Sellow* s.n. in P. Holotype not indicated by Sprengel but probably *Sellow* s.n. in B (now destroyed). Holotype of *Amphilochia acuminatula* Gardn.: Gardner 374 in BM.

Distribution: Zone of the atlantic coastal rain-forests of Brazil.

BRAZIL, Espírito Santo: Between Campos and Victoria, *Sellow* s.n.; Linhares, Rio Doce, *Kuhlmann* 108 = RB 34387. Rio de Janeiro: Orgaos Mts., *Gardner* 374; —, *Miers* s.n., 3451, 4599. Bahia: *Blanchet* 1692. Pernambuco: Igarassu, *Ridley*, *Lea* & *Ramage* s.n.

Ecology: In mountain forests; fl. Oct., March (two rep.); fr. March (one rep.).

Observation: The diagnosis of Sprengel does not cover the present species in every respect: the calyx is said to have three sepals and the corolla five petals. The other characters, however, correspond to those of the relevant species. Warming who saw the Berlin material, came to the conclusion that Sprengel's *Agardhia cryptantha* was in fact a *Qualea*. This is confirmed by the Berlin labels on the *Sellow* specimens that were sent abroad. Therefore, notwithstanding the disagreement between description and characters, the present author feels justified in accepting Warming's conclusion.

var. **marginata** (Miq.) Staf. nov. comb. *Amphilochia marginata* Miq. Linnaea 22: 796. 1849; Walp. 1851/52 p. 527; Warm. 1867 p. 27. *Qualea marginata* Warm. 1875 p. 52; — 1889 p. 23.

Leaves oblong, ovate-oblong or elliptic-oblong, apically rounded or obtuse.

Lectotype: *Blanchet* 3455 in BR. The place where Miquel's original specimen is preserved is not known. Isotypes in: BM, C, F, G, K, MO, NY, OXF, P, W. Distribution: Once collected.

BRAZIL, Bahia: Serra Jacobina, on top of the ridge, *Blanchet* 3455.

Observation: The only difference with the var. *cryptantha* is found in the shape of the leaves (generally oblong, apically rounded).

COLLECTORS' NUMBERS

The numbers in parentheses refer to the serial numbers of the species of *Qualea*. The letter a refers to the subdivision containing the nomenclatural type of the species, the letter b to the second subdivision of the respective species. The collectors' numbers printed in *italics* are not mentioned in the text.

ALLEN, P. H. 3342 (36); 3346 (18); 4645 (51). ANISITS 2024 (44); 2363 (56a); 2365 (44); 2424 (46); 2708 (56a); 2837 (44). ARCHER 7878 (22). BALANSA 2014 (56a); 2014a (56a). BANG 1663 (46). BARRETO 1705 (58); 7125 (44); 7128 (44); 7129 (44); 7130 (44); 7132 (44); 7134 (45a); 7135 (45a); 7138 (45a); 7139 (46); 7140 (46); 7142 (46); 7147 (46); 7148 (46); 7149 (56a); 7151 (56a); 7152 (56a); 8514 (45b); 8816 (46); 9245 (56a); 9309 (54a); 9750 (46); 12133 (54a); 12134 (46). BENOIST 187 (29); 1564 (34); 1604 (22). BLACK, G. A. 48–2664 (24). BLACK & FORSTER 48–3348 (22). BLANCHET 1692 (59a); 2808 (46); 3081 (44); 3455 (59b). BOSCHBEHEER 12 L (22); 48 (7); 53 (47). B.B.S. II (22); 171 (29); 405 (22); 600 (22); 1011 (22); 1015 (22); 1016 (22); 1024 (47); 1040 (47). B.W. 738 (47); 1346 (22); 1372 (22); 1425 (7); 1501 (47); 1694 (22); 1761 (29); 1861 (22); 1884 (22); 2144 (7); 2328 (7); 2394 (47); 2462 (7); 2479 (29); 2814 (47); 3784 (22); 3811 (47); 4017 (22); 4173 (47); 4260 (29); 4287 (22); 4320 (47); 4331 (22); 4914 (47); 4928 (7); 5451 (22); 5511 (22); 6019 (47); 6220 (7); 6336 (29); 6338 (22). BRADE 15472 (44). BURCHFELL 4278 (56a); 5214 (45a); 6008 (46); 6106 (44); 6108 (46); 6144 (45b); 7280 (46); 7591 (46); 7926 (46); 8255 (44); 8498 (44); 8520 (46). CAMPOS NOVAES 1111 (45a). CAMPANEMA RB 14061 (56a). CAPUCHO 446 (36); 488 (46). CARDENAS 2002 (45b); 2083 (24). CARDONA 1704 (39); 1762 (9); 1905 (1). CLAUSSEN: numbers

often unreliable. CONSTANTINO 152 (54b). COSTA, R. C. MONTEIRO DA 224 (46); 299 (44). CUATRECASAS 6956 (24); 14410 (30). CURRAN 169 (51). DAHLGREN 871 (44); 882 (46). DUARTE 690 (54b); 1491 (46); 2252 (56a); 2751 (56a). DUARTE DE BARROS 53 (19). DUCKE 46 12; 55 24; 61 12; 221 (RB 34660) (6); 227 (6); 336 (RB 34662) 42; 668 33; 992 5; 1061 3; 1063 28; 1064 (35); 1277 6; 2183 (46). PG numbers. Musco Goeldi: PG 3585 (RB 14068) (44); PG 6922 (6); PG 7991 47; PG 8001 5; PG 8159 (44); PG 9028 (47); PG 9610 (13); PG 11261 47; PG 11425 5; PG 11546 (RB 14060) (6); PG 14869 (RB 5730) (5); PG 15491 (7); PG 15006 (47); PG 15509 (13); PG 15547 (36); PG 15550 7; PG 15641 47; PG 15658 36; PG 15669 5; PG 15795 (RB 5725) 27b; PG 15890 (RB 8345) 28; PG 15897 47; PG 15975 (RB 8455) (13); PG 15978 24; PG 16143 5; PG 16427 36; PG 16455 (RB 8420) 22; PG 16491 (RB 8422) 5; PG 16559 (RB 8461) 7; PG 16593 (RB 13699) (24); PG 16666 (5); PG 17027 (7); PG 17286 (RB 13698) (24). — RB numbers (Jardim Botânico Rio de Janeiro): RB 5725 (PG 15795) 27b; RB 5730 (PG 14869) (5); RB 8345 (PG 15890) (28); RB 8420 (PG 16455) (22); RB 8422 (PG 16491) (5); 8455 (PG 15975) (13); RB 8461 (PG 16559) (7); RB 13695 (47); RB 13698 (PG 17286) (24); RB 13699 (PG 16593) 24; RB 14060 (PG 11546) (6); RB 14068 (PG 3585) 44; RB 17742 15; RB 17761 24; RB 17762 (24); RB 17775 (22); RB 18372 57; RB 20566 36; RB 21289 19; RB 23485 36; RB 23486 (7); RB 23487 5; RB 23488 24; RB 23489 12; RB 23791 (50); RB 23793 (3); RB 24160 35; RB 24161 42; RB 24165 43; RB 34660 (Ducke 221) (6); RB 34662 42; RB 34663 46; RB 34664 50; RB 34665 18; RB 34666 (20); RB 34667 41; RB 34668 10; RB 34669 16; RB 34671 (17); RB 34674 (49). DUSEN 35 41 44; 9655 44; 10466a 56a; 10559 56a; 11287 (44); 11649 (56a); 11724 (45a); 11725 (56a); 11748 (56a); 16438 (44); 16506 (45a); 16507 (56a). FERREIRA 530 (36). FIEBRIG 517 (56a); 4013 (4964) (46); 4465 (44); 5147 (56a); 6363 (56a). FOREST DEPT. BRIT. GUIANA 832 (36); 2827 (39); 2832 (31). FROES 11712 (46); 21443 (2); 21577 (46); 21616 (6); 22377 (17); 22378 (24); 22389 (42); 22758 (6); 22759 (6); 23034 (47); 23760 (24); 24248 (46). FROES-KRUKOFF 2029 (22). FUNCK & SCHLIM 637 (37). GANDOGER 100 (29). GARDNER 374 (59a); 1597 (46); 2162 (44); 2163bis (44); 2841 (4); 3143 (44); 3144 (45b); 3144 (46); 3145 (46); 3146 15b; 4554 54a; GAUCHAUD 305 45b; 715 (44); 857 (45a). GLAZIOU 2113 57; 2567 57; 2926 57; 3956 45b; 3957 57; 6473 (57); 9416 (19); 9794 44; 10731 19; 10733 46; 12662 (46); 12663 (56a); 12664 (54b); 12664a (55); 13808 (46); 13810 (6); 14695 (56a); 14696 (44); 14697 (52); 16766 (57); 17611 (44); 17612 (44); 17613(45a); 19147 (57); 19148 (45a, b); 19149 (56a); 19150 46; 19150a 45b; 19153 25; 19154 44; 20298 (46); 20683 (44); 20684 45b; 20685 54b. GEDDES PG 1591 36. GUERRERIZ & SCHULTES 530 (20). HASSLER 3528 (56a); 3528a (56a); 5583 (44); 5590 (46); 6705 (56a); 7881, 7881a (44); 8144 (45b); 8229 (46); 8790 (56a); 10076 (44); 10242 (45b); 10692 (46); 10734 45a; 10738 45a; 12356 56a. HEMMENDORF 216 45b; 264 (44); 265 (46); 268 45a; 269 44; 286 45a. HENSCHEN (vide Regnell II 99) (45a). HILAIRE, St. 72 (19); 902bis (45b); B¹ 1360 (46); B¹ 1979 (56a); B¹ 1953bis (46); B² 2375 (44); B² 2352 (45b); B² 2353 (45b); B² 2376bis (46); B² 2359 (45a); C¹ 225bis (44); C¹ 731 45b; C¹ 732 45b; C¹ 800 (46); C¹ 1193 (53b); C¹ 1244 (56a); C² 294 (45a). HOEHNE 28397 (53a). HOLT & BLAKE 717 (10). HOSTMANN & KAPPLER, ed. HOHENACKER 1293 (22). HUBER PG 1844 (24). JAHN 500 (37); 543 (37); 1335 (37). JONSSON 387a (56a). JORGENSEN 3730 (56a). KAPPLER ed. HOHENACKER 1293 (22) (cf. HOSTMANN & KAPPLER); 2037 (7). KEGEL (herb.) 12340 (45b). KILLIP & SMITH 30204 (24). KLUG 748 (23); 4275 (48). KRUKOFF 5821 A (44); 6433 (28); 6575 (28); 7169 (24); 8834 (2); 8949 (24); 10124 (48). KUHLMANN 108 (RB 34387) (59a); 181 (RB 2926) (6); 196 (RB 34385) (38); 432 (RB 57596) (38); RB 17767 (36); RB 17769 (44); RB 34385 (38); RB 48136 (19). LANGSDORFF 822 (54a). LANJOUW & LINDEMAN 392 (29); 395 (29); 429 (22); 1195 (47); 2440 (29); 2656 (7); 2802 (29); 2920 (29). LASSER 1759 (14). LEBLOND 40 (22). LEPRIEUR 284 (24). LINDMANN A. 2729 (44); A. 3031 (46); A. 3861 (56a). LISBOA PG 2397 (46). LÖFGREN 288 (44); 320 (46); 380 (56b); 635 (46); 1089 (44). LÖFGREN & EDWALL 13537 45a; LÜTZELBURG 437 44; 2094 46; 3024 (46); 3098 (44); 3099 (44); 7219 (54a); 12492 46; 14074 44; 25880 (46); 26171 (46); 26206 (46). MACEDO, A. 1291 (46). MACEDO, O. 282 (46). MACHADO 435 (46).

MAGUIRE 24841 (7). MALME I. 1036 (46); I. 1142 (44); I. 1168 (45b); II. 1806 (46); II. 2248 (5); II. 2291 (46); II. 2380 (54b); II. 2380a (54b). MARKGRAF 3313 (54a); 3442 (46). MARTIUS 114 (44); 1181 (44). MATTHEWS 742 (59a). MELINON 10 (22); 47 (22); 49 (22); 105 (22); 142 (34); 361 (7); 390 (7). MEXIA 5581 (45b); 5639 (44); 5641 (45b); 5698 (46); 5973a (24). MIERS 3451 (59a); 4599 (59a). MIRANDA 7 (46). MONTEIRO DA COSTA, R. C. 224 (46); 299 (44). MOORE 486 (46); 740 (44). MOSEN 1270 (44); 1271 (44); 1272 (45a); 1273 (45a); 1274 (45a); 4143 (55); 4144 (45b). MOURA, DE 75 (45b). MYERS 5662 (36). NETTO 68 (44). OGCHIONI *RB 44194* (46). OLIVEIRA 163 (54b). PINKUS 61 (39); 240 (44). PIRES, J. M. 55 (6); 1441 (24). PIRES & BLACK 1693a (44); 2005 (44); 2166 (46); 2222 (44); 2309 (46); 2478 (45b); 2579 (46). PITTIER 14045 (37); 15444 (37); 15720 (37). POHL 428 (44); 574 (46); 575 (55); 2577 (56a); 2860 (45b); 3460 (56a); 3930 (45b); 3931 (46); 5848 (45a). REGNILL II. 99 (45a); III. 526 (46); III. 526 (45a); III. 527 (44); III. 528a (45b); III. 528b (45b); III. 528c (45a); III. 529 (55); III. 529* (56a); III. 1545 (45b); III. 1760 (45b). REISS 62 (56a); 63 (56a). RIEDEL 459 (45b). ROBERT 568 (46); 568b (46); 570b (44); 643 (45b). ROJAS (cf. Hassler) 10738 (45a). RORAIMA EXP. (cf. Thurn) 79 (39). SAGOT 981 (22). SAMPAIO 6843 (56a). SCHOMBURGK VII (39); 19 (9); 584 (39); 893 (39); 1047 (39); 1537 (9). SCHWACKE (herb.) III. 280 (6); III. 487 (6). SELLOW 346 (53a); 1524 (46); 2003 (46); 2015 (56a); 5252 (56b). SICK B. 24 (46). SILVA, N. T. da 88 (7); 135 (22). SMITH, A. C. 2709 (7); 3250 (47). SPRUCE 336 (44); 1132 (6); 1290 (6); 1838 (6); 2612 (24); 2706 (2); 2713 (32); 2740 (2); 3059 (50); 3289 (12); 3341 (16); 3388 (18). STEINBACH 6067 (44); 6785 (44). STOLYERMARK 57828 (11); 60028 (14); 60291 (14); 60438 (14); 60490 (39); 60674 (39); 60710 (39); 60914 (14). TATE 194 (11); 206 (39); 915 (8). TESSMANN 3451 (48); 4291 (36); 4465 (35); 4855 (26). THURN, Im ("Roraima Exp.") 79 (39). ULE 59 (46); 69 (54b); 325 (45b); 326 (44); 7316 (56b); 8627 (39); 8883 (6). VAUTHIER 429 (56a). VECCHI 408 (56a). VIEGAS 5548 (44). WACHENHEIM 49 (22); 125 (22); 205 (22). WEDDELL 1594 (44); 1610 (44); 1936 (44); 2167 (46); 2500 (46); 2596 (46); 2817 (45b); 2832 (44); 4214 (46). WEIR 385 (56a). WILLIAMS, L. L. 14384 (39); 14636 (12); 14830 (39); 15063 (11); 15728 (16). WILLIAMS L. O. 5439 (56b). WILLIAMS, R. S. 397 (45b); 528 (44); 1575 (44). Woodherbarium Suriname 31 (7); 59, 59a (47); 95, 95a (7); 333 (22). ZEHNTNER 402 (46).

VERNACULAR NAMES

The numbers refer to the serial numbers of the species of *Qualea*

Amu-ricu-wai-yek	14	Lacreiro	36
Angelica	38	Louro-tinga	45
Ariuaú	44	Mandioqueira	5, 7
Arvore de terra	44	Merindiba bagre	58
Bergkwarrie	29	Minchorai-yek	14
Burro-caá	56	Mirabau do Varzea	24
Carvalho brasileiro	54	Muneridang	22, 29
Cascudo	54	Pao terra	cf. Pau terra
Cèdre gris	29	Páu de judeu	46
Cèdre jaune	29	Páu de Mastro	22
Cinzeiro	45	Páu Santo	44
Copai-yek	14	Páu de Tucano	45
Couaie	22	Páu Mulato	47
Craiba	46	Páu terra or Páu-Terra (and com- positions)	44, 45, 46, 56
Dedaleiro(a) preto(a)	56	Quaruba	47
Gronfoloe	7, 22	Quebracho falsa	56
Guiariuba	22	Umiri-rana (Umiry-rana)	5, 6
Iriakopi (Jakopi)	7, 22, 29	Uva Puva do Campo	44, 45
Judeu	46	Wassie wassie kwarrie	47
Jundiahy	45	Watra Kwarrie	22
Keu-pau-rik-orai-yek	14		
Kwarie	7		

SPECIFIC AND INFRASPECIFIC NAMES

The numbers refer to the serial numbers of *Qualea* under which the respective names are cited. The names printed in *italics* are synonyms; those printed in **bold face** type refer to new taxa.

<i>Agardhia</i>			<i>ingens</i> Warm.	27
<i>cryptantha</i> Spreng.	59		var. duckei Stäfl.	27
<i>grandiflora</i> Spreng.	44		var. <i>ingens</i>	27
<i>Amphilochia</i>			<i>jundiahy</i> Warm.	45
<i>acuminatula</i> Gardn.	59		<i>lanceifolia</i> Ducke	35
<i>cordata</i> Mart.	56		lineata Stäfl.	30
<i>cryptantha</i> Warm.	59		<i>lundii</i> (Warm.) Warm.	52
<i>dichotoma</i> Mart.	54		<i>macropetala</i> Spruce ex Warm.	32
<i>lundii</i> Warm.	53		<i>macroptera</i> A. Dietr.	45
<i>marginata</i> Miq.	59		<i>magna</i> Kuhlmann	33
<i>Lozania</i>			<i>marginata</i> Warm.	59
<i>grandiflora</i> Schult.	44		megalocarpa Stäfl.	58
<i>Qualea</i>			<i>melinonii</i> Beckmann.	29
<i>acuminata</i> Spruce ex Warm.	24		<i>microphylla</i> Warm.	19
<i>albiflora</i> Warm.	7		<i>multiflora</i> Mart.	45
<i>amoena</i> Ducke	28		var. <i>glabra</i> Mart.	45
<i>arimbacae</i> Ducke	5		ssp. <i>multiflora</i>	45
belemnensis Stäfl.	13		var. <i>pubescens</i> Mart.	45
brevipedicellata Stäfl.	33		ssp. pubescens (Mart.) Stäfl.	45
<i>calantha</i> Pilger	26		nitida Stäfl.	8
<i>calophylla</i> Pittier	37		<i>obtusata</i> Briq.	16
<i>cassiquiarensis</i> Spruce ex Warm.	12		<i>paraensis</i> Ducke	36
var. <i>belemnensis</i> Ducke	13		<i>parviflora</i> Mart.	46
clavata Stäfl.	3		var. <i>discolor</i> Mart.	46
<i>coerulea</i> Aubl.	22		var. <i>glabrata</i> Mart.	46
<i>cordata</i> Spreng.	56		var. <i>tomentosa</i> Mart.	46
var. <i>cordata</i>	56		<i>pilosa</i> Warm.	45
var. <i>grandifolia</i> Warm.	56		polychroma Stäfl.	31
var. intermedia (Warm.)			<i>psidifolia</i> Spruce ex Warm.	50
Stäfl.	56		<i>pulcherrima</i> Spruce ex Warm.	18
forma <i>rupestris</i> Hassler	56		<i>retusa</i> Spruce ex Warm.	6
<i>cryptantha</i> (Spreng.) Warm.	59		var. <i>coriacea</i> Ducke	16
var. <i>cryptantha</i>	59		rigida Stäfl.	9
var. marginata (Miq.) Stäfl.	59		<i>rosea</i> Aubl.	29
<i>cyanea</i> Ducke	43		rubiginosa Stäfl.	1
<i>cymulosa</i> Schery.	51		<i>rupicola</i> Ducke	49
<i>decorticans</i> Ducke	41		<i>tessmannii</i> Mildbr.	48
<i>densiflora</i> Warm.	55		<i>themistoclesii</i> Ducke	17
<i>dichotoma</i> (Mart.) Warm.	54		<i>trichanthera</i> Spruce ex Warm.	2
var. <i>dichotoma</i>	54		<i>tricolor</i> Benoist	34
var. elongata (Warm.) Stäfl.	54		tuberculata Stäfl.	40
<i>dinizii</i> Ducke	47		<i>schomburgkiana</i> Warm.	39
var. <i>glabrifolia</i> Meurs ex Amsh.	47		<i>selloi</i> Warm.	53
<i>ecalcarata</i> Mart.	44		ssp. pubescens Stäfl.	53
<i>elegans</i> Taub. ex Benoist	25		ssp. <i>selloi</i>	53
<i>elongata</i> Warm.	54		<i>speciosa</i> Huber	24
<i>esmeraldae</i> Standl.	11		<i>sprucei</i> Warm.	21
<i>ferruginea</i> Steyermark	14		<i>subvillosa</i> Link ex A. Dietr.	45
<i>gardneriana</i> Warm.	4		var. <i>glabrifolia</i> A. Dietr.	45
<i>gestasiana</i> St. Hil.	19		<i>suprema</i> Ducke	42
<i>glaberrima</i> Ducke	7		urceolata Stäfl.	15
<i>glaucæ</i> Warm.	54		verruculosa Stäfl.	10
<i>glaziovii</i> Warm.	57		<i>violacea</i> Mart. & Zucc. ex Schult.	29
<i>gracilior</i> Pilger	35		<i>virgata</i> Rusby	45
<i>grandiflora</i> Mart.	44		<i>wittrockii</i> Malme	5
<i>homosepala</i> Ducke	20			
<i>impexa</i> Macbride	23		<i>Schuechia</i>	
intermedia Warm.	56		<i>brasilienis</i> Endl. ex Walp.	44
			<i>ecalcarata</i> Warm.	44

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ARCHITECTURE AND GROWTH OF THE
PRIMARY CELL WALL IN SOME PLANT HAIRS AND IN
THE PHYCOMYCES SPORANGIOPHORE

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INTRODUCTION

Electron micrographs of the primary cell wall in the growth-zone of *Phycomyces* sporangiophores show an isotropic network of chitin fibrils on the outside and an almost transverse structure on the inside (3, 8). The same applies to the cellulose fibrils in the cell wall of staminal hairs of *Tradescantia* (10). Axial orientation of the outer fibrils is apparent in the primary cell wall of growing cotton hairs, which on the inside again show a more or less transverse structure (5, 9).

The present paper reports the finding of a similar architecture in the growing hairs of two more plant species, viz. *Ceiba pentandra* var. *caribaea* and *Asclepias cornuti*. Furthermore some new E.M.-graphs of cotton hairs are presented, since those published earlier were of a low standard. Obviously because the present E.M.-graphs revealed more details, we were struck by a particular common feature in the fibrillar structure which led to some deductions regarding the process of cell wall extension in plant hairs and in the *Phycomyces* sporangiophore. These will be discussed in the last section.

METHODS

Fruits, gathered at definite intervals after flowering, were preserved in alcohol*.

If the hairs of young fruits were viewed in radial direction between crossed nicols, a negative double refraction with reference to the cell axis was found. This always occurs in growing tubular cells, at least in growing regions of such cells. Of course, hairs of nearly full-grown fruits were always entirely positive.

With *Ceiba*, negative double refraction was found in the sample of 25 days and in all younger ones, the next sample being 35 days old.

* We are greatly indebted to the manager of Siloewok Sawangan estate, Java, who furnished the *Ceiba* material. *Asclepias* and cotton were grown in our botanical garden.

In order to be sure that the sample to be used for the electronmicroscopy would contain primary cell walls only, fruits gathered ca 20 days after flowering were taken. The mean hair length was roughly 12 mm as against 25 mm in the 35 days sample.

The *Asclepias* hairs were negatively birefringent up to 35 days, though less distinctly than after 28 days. Hairs of 21 days old were used for the E.M.-work. Like those of *Ceiba* they were negative from the extreme tip down to base. Their length was 8 mm as against 30 mm in the 35 days sample.

The cotton hairs used, were 15 days old and were from the same fruits as used in earlier work (9). Of these hairs too, the extreme tips were negatively birefringent.

The hairs were cut off, suspended in 70 % ethanol and cut into pieces of 30–60 μ length by means of a small electric blender. The ethanol and all other liquids used, had previously been freed from dust, etc. by centrifuging.

The fragmented hairs were centrifuged and then cleaned by the following successive treatments, alternated with centrifuging in water:

- a. 30 min. in perhydrol-glacial acetic acid 1:1 at 100° C,
- b. 20 min. in 2 % sulfuric acid at 100° C,
- c. 20 min. in 2 % NaOH at 100° C,
- d. neutralisation and frequent washing with water.

The cleaned fragmented hairs were mounted on collodion covered E.M. grids and shadowed with Pt.

RESULTS

The similarity of the architecture of the primary cell wall of hairs from *Ceiba* (figs 1, 2), *Asclepias* (figs 3, 4, 5, 6) and *Gossypium* (figs 7, 8) is very striking indeed. There is, in fact, no difference whatsoever.

Especially with a more or less transverse direction of shadowing, as in figs 2, 4 and 8, it is clear that the outermost fibrils are roughly axial. Even if the direction of shadowing is also nearly axially, this is apparent (figs 1 and 7). Since the hairs very probably shorten during the chemical treatment, the axial orientation will be more marked in vivo. Often several fibrils are combined to bundles (fig. 8). In all the E.M.-graphs, but in particular in figs 2, 7 and 8, one can see that in a deeper layer the fibrils run in an oblique direction and that in a still deeper layer a transverse direction predominates.

Accordingly, a transverse structure is very conspicuous on the inside of the primary cell wall, as is clearly demonstrated by figs 1, 3, 5 and 7. This stratum is of considerable thickness and the fibrillar structure is more compact than on the outside. Hence, one rarely sees the obliquely or axially oriented fibrils underneath, e.g. in the frayed-out cell wall edge in fig. 6.

Obviously, there is a gradual change from a compact transverse structure on the inside to a loose, more or less axial structure on the outside of the growing cell wall.

Not only the fibril orientations, also the interfibrillar spaces differ on the two sides. Figs 3, 5 and 7 show numerous transversely oriented tiny meshes on the inside of the cell wall. Hence, the fibrils, or bundles of these, show a wavy structure, which is very conspicuous in fig. 7. There are no broken fibrils and apparently, the meshes have originated by a pushing or drawing apart of the fibrils rather than by tearing the cell wall or breaking the fibrils. The internal surface of the cell wall resembles a submicroscopic fishing-net with transversely elongated meshes. These are roughly 200–500 Å wide and 1000–1500 Å long. Their depth varies even more considerably, but in many cases it will be more than the total thickness of several fibrils. Usually one can see one or more fibrils at the "bottom" of the meshes, running in oblique or axial direction, which demonstrates that the meshes do not perforate the cell wall but are confined to a stratum of it.

After having observed the meshes on the inside of the cell wall, a look at the outside (figs 2, 4, 7 and 8) makes clear that here as well one might speak of meshes, though larger and axially elongated ones. Moreover, they are confined to a very thin superficial stratum. Their mean width corresponds roughly with the mean length of the transversely elongated meshes on the interior surface of the cell wall, but their lengths vary considerably.

DISCUSSION

If the architecture of the growing hairs of *Ceiba*, *Asclepias* and *Gossypium*, is compared with those of *Tradescantia* staminal hairs (10) and of the primary cell wall of the *Phycomyces* sporangiophore (8), the only difference seems to be that in the latter two cases the outermost fibrils are oriented at random instead of axially. However, since the sporangiophore shortens considerably on loss of turgor and during the chemical treatment, it is probable that in vivo a small preference for axial orientation occurs. Quite apart from that, the structural difference between the inside and the outside of the cell wall is "analogous", viz. likewise indicating an extension of the transverse structure of the inside.

Meshes, similar to those described here, are also visible on the E.M. graphs of *Tradescantia* and *Phycomyces*. They are less conspicuous, probably merely because the E.M. graphs show less details.

This similarity of the fibrillar architecture of the growing cell walls of all these cells, belonging to widely different plant families, must have a common cause, in all probability: the manner of cell wall extension. Thus, the question arises how these cell walls grow.

First we should discuss whether the manner of cell growth as has recently been described for other plant cells, might possibly occur in the cells under consideration.

In parenchyma cells and epidermal cells of *Avena* coleoptiles, tip growth has been demonstrated (6). This was also found in cambium cells (1) and in *Spirogyra* (2, p. 283). The authors state that the tips of the cells are opened and that the cytoplasm apparently oozes out of the cell. It weaves its wall. First, more or less longitudinal fibrils

are deposited. These act as a kind of warp and are interwoven with a weft of mainly transverse fibrils, which soon outnumber the longitudinal ones, thus producing the negative birefringence of the fully grown primary cell wall. The unfinished cell wall, however, is either isotropic or positively birefringent with reference to the cell axis. In view of the following discussion we wish to emphasize this optical behaviour.

In other areas of the same parenchyma and cambium cells, growth is not such an addition of new cell wall areas, but it is a true cell wall extension, presumably due to a pushing apart of fibrils by local plasmatic growth. In these spots the cellulose structure is completely perforated temporarily. These perforations have dimensions of $\frac{1}{4}$ –1 μ . Soon new fibrils are inserted. This kind of intussusception growth was also discovered by FREY-WYSSLING and his collaborators and named mosaic-growth (1, 4).

Does tip growth occur in the *Phycomyces* sporangiophore and the plant hairs under consideration?

Obviously not in the sporangiophore when the latter carries a sporangium. Neither can there be any question of similar addition of large pieces of cell wall in the growing regions below the sporangium. Firstly the electron microscope nor the studies on the distribution of growth in the growth-zone ever revealed such local differences. Secondly, the whole growth-zone shows a negative double refraction of a very uniform intensity. Thirdly, a perforation of the cell wall of such a turgid cell, surrounded by air, is quite inconceivable. The same conclusion applies to the sporangium-free growth stage of this sporangiophore. Admittedly, its apex grows, but in the same manner as the rest of the growth-zone and not in the manner of typical tip-growth, for the whole growth-zone including the extreme tip is negatively birefringent (3).

Neither can there be tip-growth or any other similar addition of new pieces of cell wall in growing *Tradescantia* staminal hairs. Firstly, the hair is a chain of cells and the cells cannot have growing tips. Secondly, the cells are negatively birefringent throughout, even immediately after cell division (10). Here too, perforation of the cell wall by protoplasm obviously is out of the question.

Whether the hairs of cotton, *Ceiba* and *Asclepias* grow at their apex only, or over their full length, seems uncertain. Generally with cotton, the latter type of growth is taken for granted. Some authors assume tip growth, but as far as we know, nothing has been proven. Anyway, if solely the apex grows in these cases, the sequence of deposition of a "warp" and — later on — the interweaving of a "weft", as is typical for tip-growth, does not occur here either. Firstly, we have observed that the extreme cell apices in all these cases are negatively birefringent like the rest of the cell wall of the growing cells. Secondly, the axial and the transverse fibrils are not interwoven, but occur in different layers.

Typical mosaic-growth, characterized by rather few, but large perforations, as found in the cell wall of parenchyma- and cambium

cells, apparently does not occur in hairs, nor in the *Phycomyces* sporangiophore, for such conspicuous perforations would not have escaped notice on the E.M.-graphs.

Therefore, the conclusion is inescapable that the complicated fibrillar structure of the cell wall as revealed in the E.M.-graphs of the plant hairs and the *Phycomyces* sporangiophore, was in the act of extending at the moment of fixation. This clearly means that we have come across a third type of cell wall extension, which is characterized by the occurrence of a great number of shallow submicroscopic tears or meshes, uniformly distributed in the cell wall in all growing regions of the cell and varying in shape and area in the different layers of the cell wall, the latter therefore never being perforated. Unlike the perforations occurring during mosaic-growth, these meshes never seem to be filled in with fibrils (at least not completely), but to persist and extend. Probably they are filled in with non-fibrillar material and the very small holes visible in the cell wall, e.g. in fig. 8, will not be true perforations.

To attain a dynamic picture of this type of cell wall extension, an assumption must be made. We think that although plasm threads probably will occur in deeper layers of the cell wall, the majority of new fibrils will be deposited on the inside, adjacent to the outer protoplasm layer. Since the outer layers of the cell wall will be incrustated with cutin and wax, one can hardly expect fibrils growing or being inserted here. Apparently these new fibrils are deposited in a nearly transverse direction. Most probably, the fibrils are never strictly parallel, but interwoven or rather intertwined with their "contemporaries". In the growth-zone of the *Phycomyces* sporangiophore the mean direction is according to a flat spiral.

Our conception of the manner of extension of this cell wall is as follows. Owing to cell wall tension and, may be, assisted by local plasm growth into the cell wall, the small bundles of newly deposited, intertwined fibrils occurring on the inside of the cell wall will be split locally, thus producing the transversely oriented superficial meshes. Since these meshes are not filled in with new fibrils, axial cell wall extension elongates them more and more in axial direction. Meanwhile new fibrils are deposited on the inside and the extending mesh is therefore gradually shifting to the outside of the cell wall, probably being more and more filled in with incrustating materials. The greater the ultimate extension, the more axial the fibril orientation on the outside will be. Since the hairs of the samples used, had not yet acquired their full length, the axial orientation probably will be even more conspicuous in older hairs. Even hairs of one fruit may differ in age, hence will show minor structural differences. As will be evident, the occurrence of random orientation on the outside of the *Tradescantia* staminal hairs and the *Phycomyces* sporangiophore is to be considered as a quantitative and hence irrelevant difference.

Fig. 9 (left part) very schematically illustrates the essential part of our theory.

Our conception readily explains some additional structural details,

already mentioned. The diameter of the cells under consideration, keeps practically constant during growth. So, if the meshes visible on the outside, have originated from meshes similar to those occurring on the inside, the transverse dimension of both should be roughly equal. This lines up with the facts. However, the mean circumference

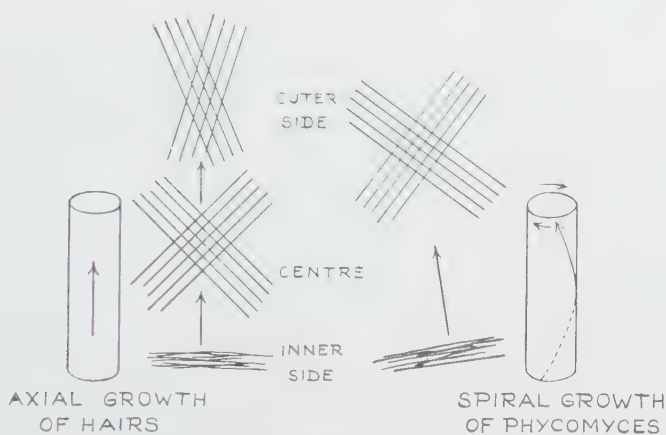


Fig. 9. Scheme of multi-net-growth in the upper cell wall of a tubular cell in connection with growth-direction and rotation of the apex.

of the meshes greatly increases. This means that the fibrils occurring in one bundle, are not fixed to each other, but may shift somewhat. What appears as one mesh on the inside, is subdivided in several axially elongated meshes on the outside. As a matter of course these will be more shallow than those on the inside and the fibrillar structure will moreover be much looser than on the inside. This is clearly visible.

We propose for this type of growth the name *multi-net-growth*, since the cell wall may be compared with a sheaf of fishing-nets which gradually change in mesh and in direction of the twine. In reality, of course, the "nets" are not separated, but extensively interwoven. There are no distinct layers, but a gradual change in structure.

If our conception is right, this is *apposition-growth* if one considers the fibrillar material only, but it is *intussusception-growth* if one considers the incrustating material which fills in the meshes.

We are aware that the name *multi-net-growth* simplifies the reality, but it has the merit of stressing the most characteristic feature. In our previous publications on cell wall structure of growing cells the reversion of the fibrillar orientation was explained in a similar manner, except that the occurrence and behaviour of the meshes had not yet been noted. It was assumed that these were filled in with fibrillar instead of non-fibrillar material. The principle of reversion of fibrillar orientation on cell wall extension is by no means new, since it was postulated by J. BONNER as early as 1936.

We wish to point out that *multi-net-growth* in a tubular cell with

a flat spiral structure, as occurs in *Phycomyces* sporangiophores (8), will produce rotation of the free top (spiral growth) as a matter of course. This will be evident after examination of fig. 9 (right part).

Several years ago, one of us (7), has advanced evidence for the view that this spiral growth is partly due to the purely mechanical effect of the stretching of a flat spiral structure and partly to a process of "active intussusception" of fibrils, governed by protoplasm. We now have a better notion of the latter process. It is not an intussusception of fibrils, but the creation of the meshes and perhaps the deposition of non-fibrillar material into these.

In explaining the spiral growth of *Phycomyces* sporangiophores, FREY-WYSSLING (2, p. 305), postulates a "circular traveling of the intercalary growth" in the growth zone. However, as was already stated, there are no localized growth spots. Moreover, if there were, their supposed circular traveling would merely produce circumnutation instead of rotation of the apex.

The suitability of multi-net-growth and the unsuitability of "mosaic-growth" and "tip-growth" for cells with aerial growth, is obvious. In *Phycomyces* sporangiophores a turgor pressure of 2 atm. has been found (7). This pressure must be exerted by the growing cell wall. Isn't this quite incompatible with large perforations of its fibrillar structure such as occur with "mosaic growth" as well as with "tip growth"? The latter two types of growth will very probably be confined to tissues where the cells mutually compensate their turgor pressures and where intercellular spaces are practically lacking, e.g. in primary meristems. Here, only the thick outer epidermal cell wall exerts a pressure. Admittedly, tip growth does occur in epidermal cells too (6). How this is possible without the occurrence of perforations in the outer cell wall, is not yet quite clear. Maybe, perforations only occur in the radial and the inner-tangential cell walls, the outer cell wall probably showing multi-net-growth.

In young xylem cells BOSSHARD (1) has seen mosaic-growth and tip-growth, but he also remarks (p. 494): "In Abb. 19 ist eine junge Xylemfaser abgebildet, in der die Wachstumsbezirke nicht scharf gegeneinander abgegrenzt sind, sondern es scheint, wie wenn in diesem Falle eine grössere Fläche gleichzeitig am Wachstum teilnehme". He also describes primary cell walls as having several interwoven layers with different orientation (p. 489). Possibly, multi-net-growth or some analogous type of growth also occurs in young phloem and xylem cells.

ACKNOWLEDGEMENTS

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SUMMARY

The cellulose fibrils on the interior surface of the primary cell wall of growing hairs of *Ceiba*, *Asclepias* and *Gossypium* are oriented more

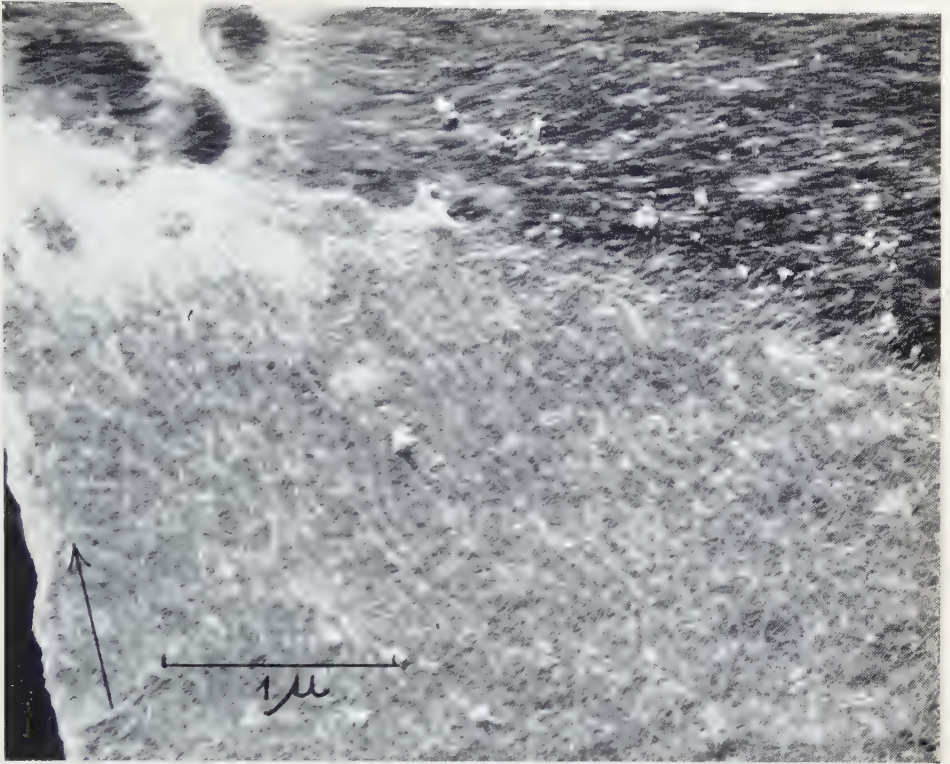


Fig. 1. *Ceiba pentandra* hair, outer and inner side top) of primary cell wall.

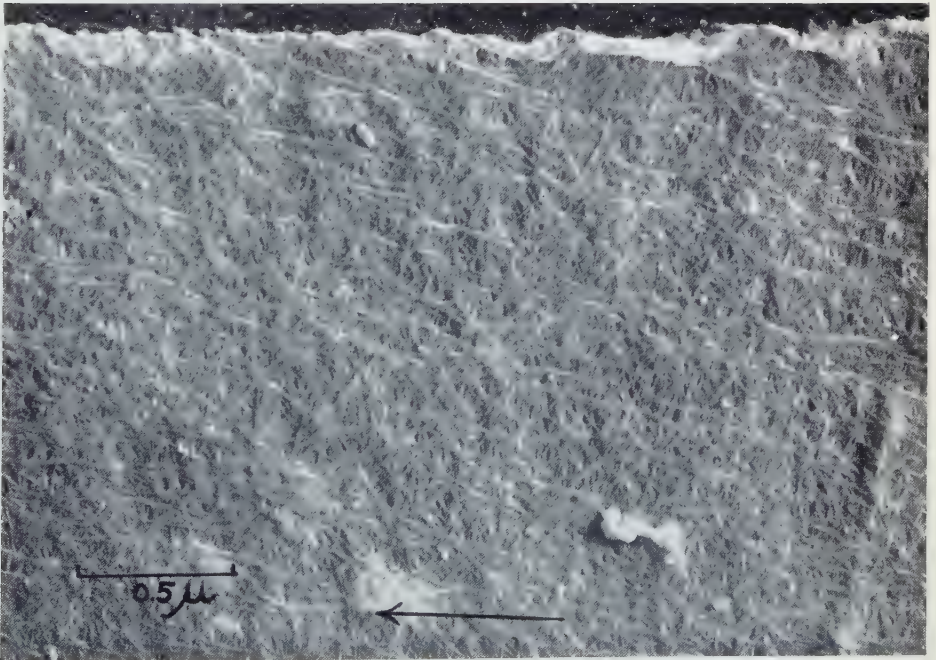


Fig. 2. *Ceiba pentandra* hair, outer side of primary cell wall.

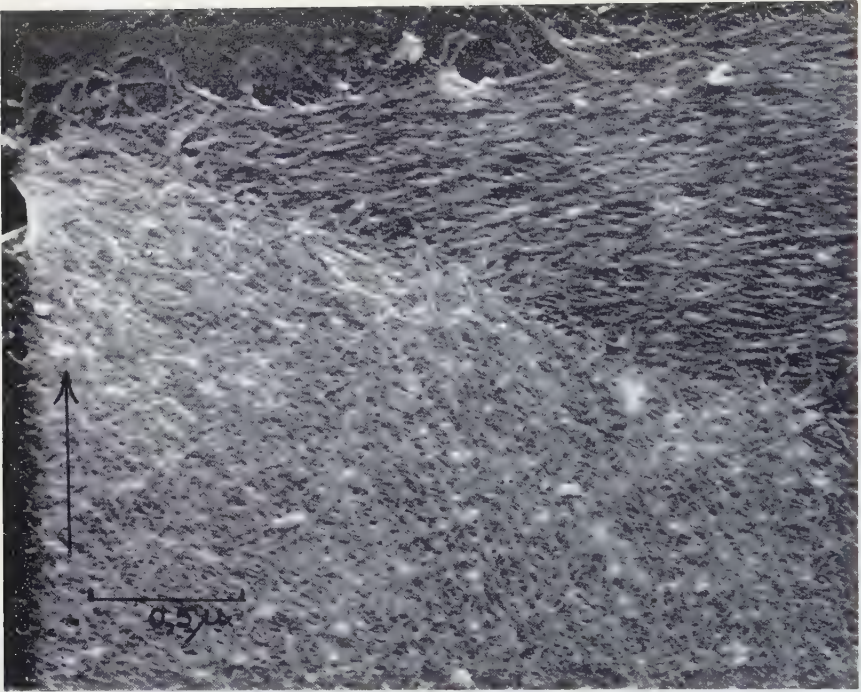


Fig. 3. *Asclepias cornuti* hair, outer and inner side top of primary cell wall.

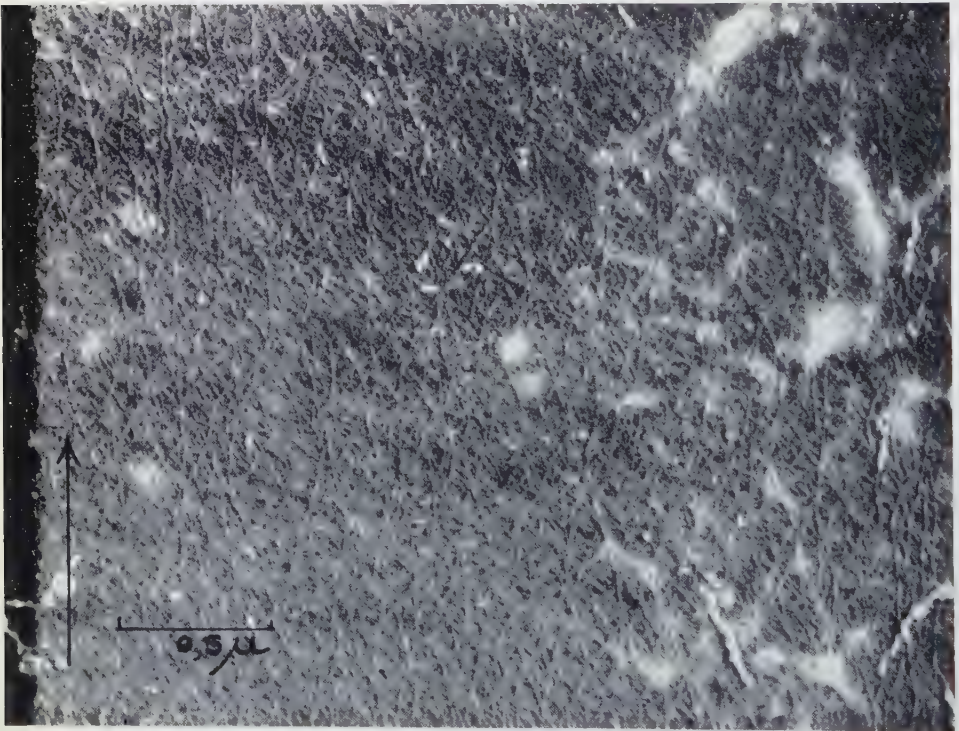


Fig. 4. *Asclepias cornuti* hair, outer side of primary cell wall.

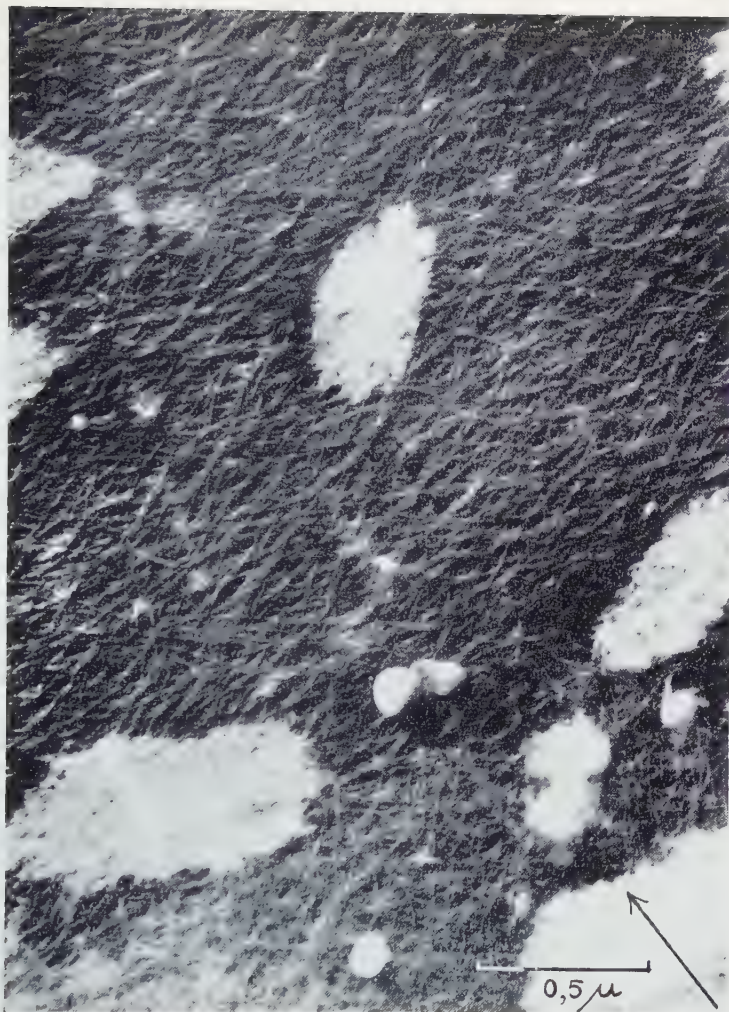


Fig. 5. *Asclepias cornuti* hair, inner side (top) and outer side (bottom) of the primary cell wall. Cell axis indicated.

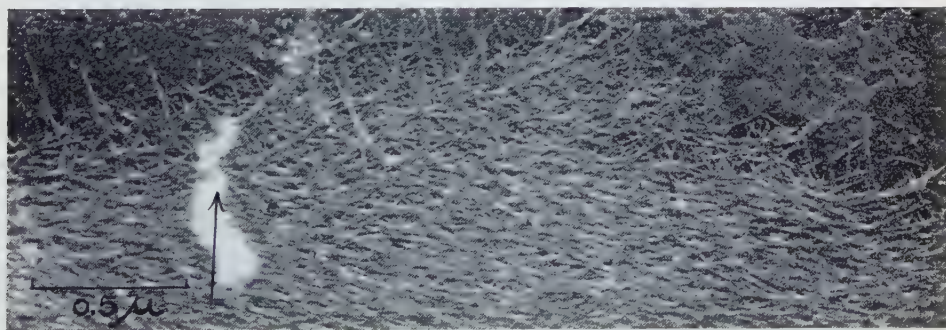


Fig. 6. *Asclepias cornuti* hair, inner side of primary cell wall. Cell axis indicated.

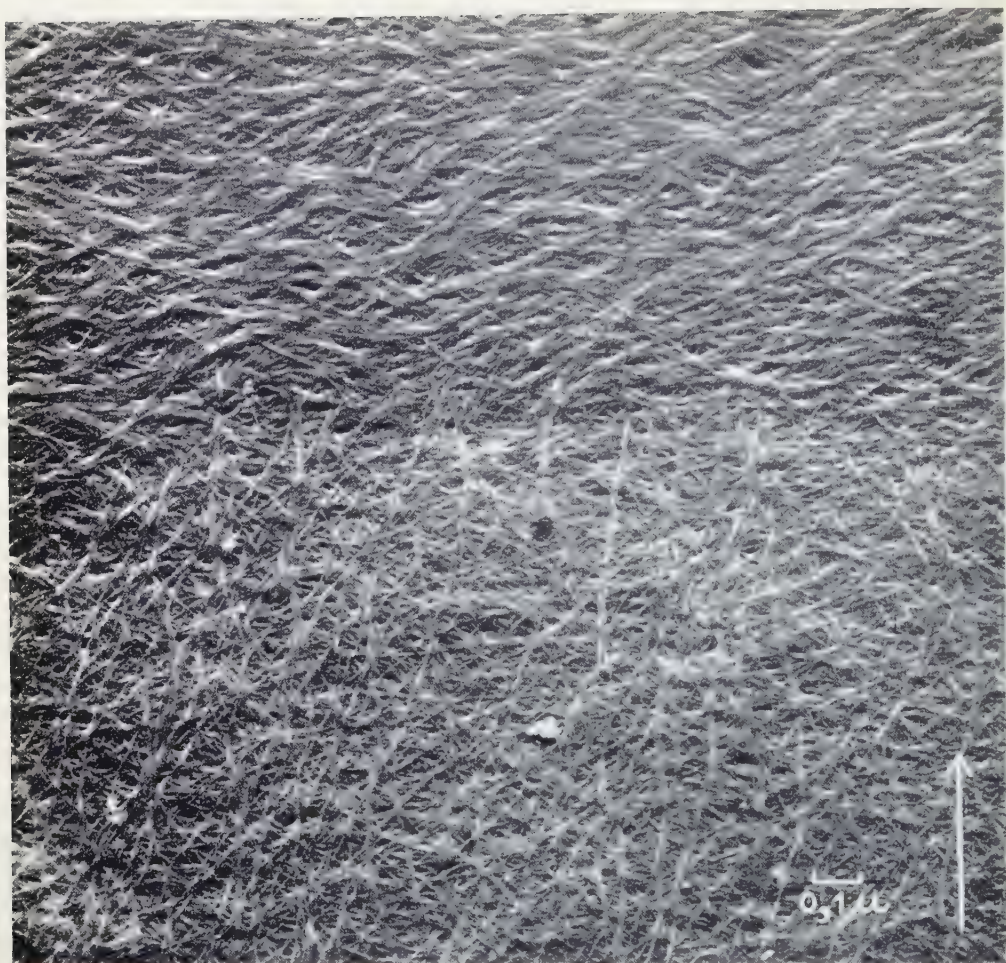


Fig. 7. *Gossypium* hair, inner side (top) and outer side (bottom) of primary cell wall. Cell axis indicated.

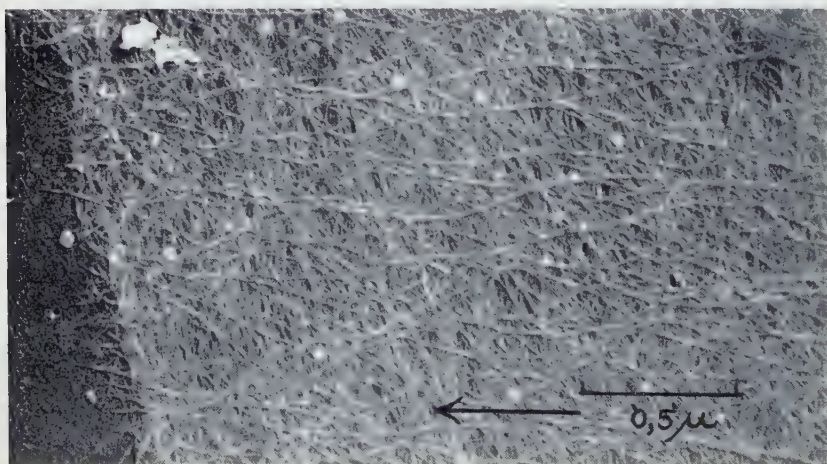


Fig. 8. *Gossypium* hair, outer side of primary cell wall. Cell axis indicated.

or less transversely. In more peripheric layers their direction changes gradually untill they are mainly axial in the outermost layer. Numerous small shallow meshes in the cell wall layers, the shapes, areas and orientation of which vary from the interior to the exterior of the cell wall suggest a new type of cell wall growth, for which the name *multi-net-growth* is proposed. In *Tradescantia* staminal hairs and in *Phycomyces* sporangiophores, an analogous architecture and obviously the same type of growth occur.

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STUDIES IN THE DISCOMYCETE GENERA CRUMENULA DE NOT. AND CENANGIUM FR.

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CONTENTS

Summary	226
Acknowledgements	227
PART I	227
a. Purpose and methods	227
b. On the taxonomy of the genus <i>Crumenula</i> de Not.	228
c. On the taxonomy of the genus <i>Cenangium</i> Fr.	229
PART II	230
Description of the fungi in relation to taxonomy and phytopathology . .	230
a. <i>Crumenula pinicola</i> (Fr.) Karst. sensu Karst.	230
b. <i>Crumenula sororia</i> Karst.	232
c. <i>Scleroderris abietina</i> (Lgbg.) Gremmen comb. nov.	234
d. <i>Scleroderris laricina</i> (Ettl.) Gremmen comb. nov.	236
e. <i>Cenangium ferruginosum</i> Fr. ex Fr.	237
f. <i>Cenangium acicolum</i> (Fuck.) Rehm	238
PART III	239
Investigations on the pathology of the fungi mentioned	239
References.	240

SUMMARY

Conifers, especially species of *Pinus*, may suffer from attack of the Discomycete genus *Crumenula*. In literature there exist many reports on the "Cenangium disease" of coniferous hosts, but it appears that the apothecia of *Cenangium ferruginosum* were often confused with the apothecia and even the pycnidia of *Crumenula*. *Cenangium ferruginosum*, however, is a common saprophyte. Representatives of both genera were thoroughly studied and an attempt was made to distinguish them even when immature. The asci and ascospores were studied, but special attention was given to the apothecial structure.

The study of the latter provided characteristic differences, on the

* The pathological part of the work was carried out by the senior author, the taxonomical part by the junior author.

basis of which it became possible to distinguish the species one from another. The necessity arose to transfer the species *Crumenula abietina* Lgbg. and *Crumenula laricina* Lttl. to the genus *Scleroderris* (Fr.) de Not.

Cultures of the fungi treated in the present paper were also studied, especially with the aim of investigating the connection between the ascigerous and the imperfect stages. Cultures were made of both ascospores and pycnosporos. A conidial form belonging to *Crumenula sororia* Karst. was newly described as *Digitosporium piniphilum* Gremmen gen. nov. spec. nov. This form was found in nature and also cultivated in vitro from ascospores. Probably it is a new member of the family of the *Excipulaceae*. Inoculations were executed with a culture of the ascospores of *Crumenula sororia*, a mono-pycnosporic culture of *Scleroderris abietina* and a mono-ascosporic culture of *Cenangium ferruginosum*. Experiments with *Cr. sororia* were successful, whilst those with *Cenangium* always failed.

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PART I

a. Purpose and methods

Representatives of both genera *Crumenula* and *Cenangium* occur on coniferous hosts and some of these species cause serious losses. When there are mature fructifications it is possible to distinguish them by means of the sporological data, but when these are lacking, identification is hardly possible. More especially, confusion is likely to occur in case of the common fungus *Cenangium ferruginosum*, the apothecia of which strongly resemble the apothecia and even the imperfect stage of *Crumenula abietina*. Apothecia of the species involved were collected and hand-sectioned. The apothecia were particularly studied with the aim of finding structural differences, whereas measurements of asci and ascospores were compared with those in literature. Moreover, culture studies were executed in the laboratory in order to observe the growth of these Discomycetes and, more especially, to investigate whether the perfect form could be obtained. The following species were studied:

- a. *Crumenula pinicola* (Fr.) Karst. sensu Karst.
- b. *Crumenula sororia* Karst.

- c. *Scleroderris abietina* (Lgbg.) Gremmen comb. nov.
- d. *Scleroderris larinina* (Ettl.) Gremmen comb. nov.
- e. *Cenangium ferruginosum* Fr. ex Fr.
- f. *Cenangium acicolum* (Fuck.) Rehm

b. *On the taxonomy of the genus Crumenula de Not.*

Review of literature

Crumenula de Not. was established by DE NOTARIS in 1863, probably based on a rediscovery of material of *Cenangium urceolus* A. et S., which he had collected on *Calluna vulgaris* Hull. NANNFELDT (16), however writes "Ob die Art de Notaris" die echte *urceolus* ist, erscheint höchst unsicher". In 1869 KARSTEN used the name *Crumenula* for a subgenus of *Peziza* (Mon. Pez. Fenn.), but in 1871 he brought it to generic rank (Myc. Fenn.) in the subfamily of the *Cenangieae*. Once more, in 1885, KARSTEN changed the name *Crumenula* to *Godronia* (Rev. Mon. p. 144), with the exclusion of *Cr. pinicola* and *Cr. sororia* which he placed in the subgenus *Heteropeziza* Fr. In 1896, REHM (18) again used *Crumenula* de Not. for the above mentioned species, *Cr. pinicola* and *Cr. sororia*, placing this genus in the *Dermateaceae* sub *Cenangieae*, together with the genera *Cenangium*, *Cenangella*, *Trybliidiella* and *Godronia*. NANNFELDT (16), in 1932, studying the genus *Crumenula*, described as a new subfamily the *Scleroderridoideae*, including *Crumenula*, *Godronia* and *Durandia* in the genus *Scleroderris* (Fr.) de Not. According to this author, there is no marked difference in the apothecial structure and he also asserts the congeniality between the imperfect stages. The type species of *Scleroderris* (Fr.) de Not. is *Scleroderris ribis* (Fr.) Lind. ETTLINGER (8) pointed out the contradictions in the arguments of NANNFELDT. The former did not observe relations with *Scleroderris*, but considered his four species of *Crumenula* a distinct group. In 1951, SEAVER (20) again transferred *Cr. pinicola* and *Cr. sororia* to the genus *Godronia* in the sense of KARSTEN (Rev. Mon. 1885).

New taxonomical conceptions on the genus *Crumenula*

In the studies by NANNFELDT (16) concerning the identity of *Crumenula* and *Scleroderris*, the taxonomy of the inoperculate Discomycetes is based on the apothecial structure. Up till now the taxonomy of the Discomycetes was mainly based on sporological data. Modern mycology should try to find a natural system based on apothecial structure, culture studies and sporology, perhaps in future combined with genetical studies.

The species *Cr. pinicola* (Fr.) Karst. sensu Karst. and *Cr. sororia* Karst. in the sense of REHM show great similarity in apothecial structure. Both possess a characteristic tissue, the *textura intricata*, as well as marginal hairs. However, inter se they differ to such an extent that it is perfectly justified to keep them separate specifically. Quite different from these two species are *Cr. abietina* Lgbg. and *Cr. aricina* Ettl. which are characterized by a *textura prismatica* whereas their apothecial structure shows a strong resemblance to that of

Scleroderris ribis (Fr.) Lind., the type species of *Scleroderris* (Fr.) de Not. Instead of marginal hairs we find some marginal scales. The ascospores are 2 — or 4 — celled, shorter than in *Scleroderris ribis* (Fr.) Lind. (Fig. 1), but not needle-shaped as in species of *Godronia* Moug. sensu REHM.

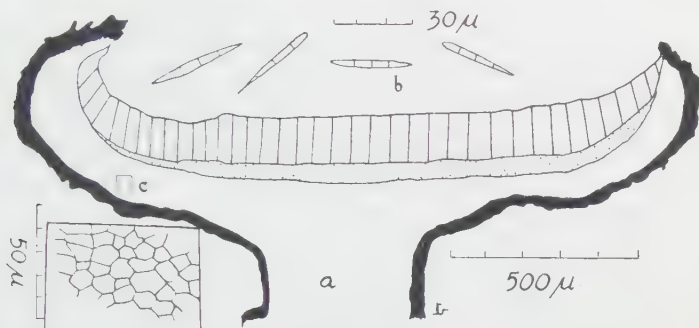


Fig. 1. *Scleroderris ribis* (Fr.) Lind. a. apothecium (partly schematic); b. ascospores; c. part of the tissue of the excipulum

Though ETTLINGER (8) proposed to conserve the name *Crumenula* sensu REHM (non *Crumenula* de Not.), in this paper, pending the conservation, alterations are not made in the name of the genus.

Up till now, the correct name of *Crumenula* sensu REHM is not known, since the junior author has not seen the type species of *Godronia* Moug., viz. *Godronia Mühlenbeckii* Moug. et Lév. and since there is no description of this species with regard to its apothecial structure. Therefore the species *Cr. abietina* and *Cr. laricina* are transferred to the genus *Scleroderris* (Fr.) de Not. on account of their apothecial structure. The species *Cr. pinicola* and *Cr. sororia* have no *Scleroderris*-characters and should provisionally remain in *Crumenula* sensu REHM.

c. On the taxonomy of the genus *Cenangium* Fr.

Review of literature

The name *Cenangium* was first used by FRIES (Syst. Myc. p. 177) in 1822 and again by KARSTEN in his *Mycologia Fennica* (p. 18 and p. 220).

REHM (18), who considered the *Cenangieae* to comprise several genera, divided *Cenangium* in the subgenera *Eucenangium* and *Encoelia*. Afterwards, most authors have accepted the same arrangement with some slight alterations, though the differences between both genera are extremely vague and difficult to define on a morphological basis.

VON HÖHNEL (12) asserted that *C. ferruginosum* Fr. ex Fr. is quite different from species of *Encoelia*. He classified this species in the *Tryblidiaceae* on account of its coriaceous structure.

Cenangium aciculum (Fuck.) REHM was placed by VON HÖHNEL in the genus *Encoelia*. This was radically altered by NANNFELDT (16), who founded the *Encoelioideae* in the *Helotiaceae* with the type genus *Encoelia* (Fr.) Karst. This subfamily is closely related to the *Ciborioideae* as

conceived by NANNFELDT on the basis of the apothecial structure. The same author was not able to classify the genus *Cenangium* Fr., so that in this case the taxonomy of REHM is still in use. The type species of this genus is *C. ferruginosum* Fr. ex Fr., as selected by NANNFELDT.

New taxonomical conceptions on the genus *Cenangium* Fr.

Because of the insufficient differences between *Cenangium* Fr. and *Encoelia* (Fr.) Karst. as to their apothecial characters, some authors use the former name, others the latter. The correct name, however, is *Cenangium* Fr., since it is the earlier name.

The junior author did not observe any characteristic difference which could serve to clearly separate both genera and therefore the fungi were studied in pure culture to see whether imperfect stages might give any clue. Always black spermogonia with bacilliform, hyaline spermatia were obtained in cultures of *Cenangium ferruginosum* Fr. ex Fr., whereas slimy sporodochia were found in the mycelia of *Encoelia fascicularis* (Fr.) Karst. These sporodochia formed globular microconidia of the same type as were also detected by DRAYTON in the genus *Sclerotinia* c.s. (DRAYTON, 1934).

The conclusions of NANNFELDT (16) on the relationship between *Encoelia* and *Ciboria* are thus confirmed by culture studies. The growth of both mycelia is so different as to safely assume that they do not belong to the same genus. In vitro, species of *Encoelia* grow rather quickly, those of *Cenangium*, however, develop very slowly. Also the colour of the mycelia is quite different. For the time being, therefore, it seems best to apply the name *Encoelia* (Fr.) Karst. to quickly growing species with slimy groups of microconidia and *Cenangium* Fr. to slowly growing fungi.

PART II

Description of the fungi in relation to taxonomy and phytopathology

a. ***Crumenula pinicola*** (Fr.) Karst. sensu Karst., Myc. Fenn. I. p. 210: 1871.

Description (after 118)

Apothecia about 1.5–2 mm across. Stipe short, 150–190 μ . The excipulum consists of two layers with a reddish brown colour (textura intricata). The first layer has a compact tissue of 30–40 μ ; the second layer a tissue with large cavities, 80–120 μ thick. The excipulum-wall, 70–100 μ thick, is also made up of a compact structure which further externally becomes quite opaque, bearing cell-protuberances on the outside. At the margo red-brown hair-like excrescences are found. Hypothecium 10–15 μ thick, colourless. Hymenium about 70 μ thick, beige-coloured. Epithecium wanting. Asci 75 \times 9–11 μ . Ascospores 17.1–30.4 \times 3.8–4.8 μ , colourless, 1- and 2-celled, markedly acuminate. Paraphyses filiform. (Fig. 2).

Culture results

Many isolates were obtained from ascospores which had naturally been ejaculated. The colour of the mycelium strongly resembled that of *Cr. sororia* Karst. varying from grey to greyish brown on cherry decoction agar. Many cultures were studied on different media, but

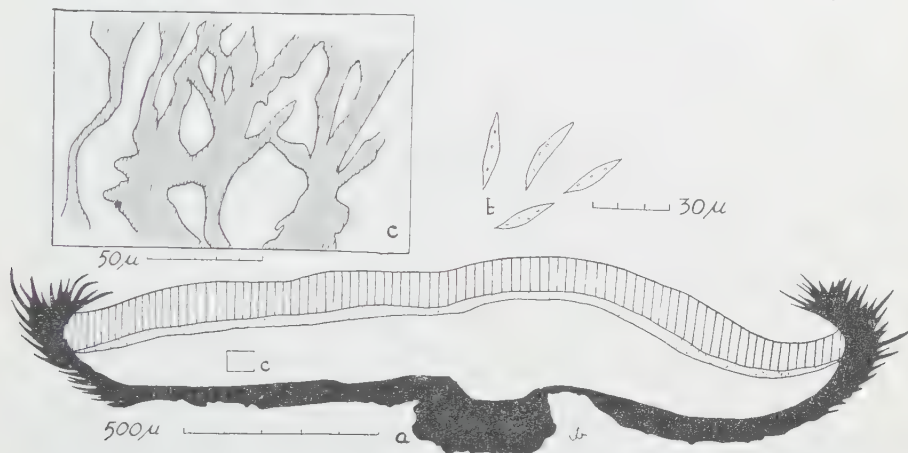


Fig. 2. *Crumenula pinicola* (Fr.) Karst. sensu Karst. a. apothecium (partly schematic); b. ascospores; c. part of the tissue of the excipulum

the junior author failed to find an imperfect stage of this Discomycete. On sterilized wheat-grains mixed with small bits of branches of *Pinus*, dark brown bodies were seen to develop after about 4 months culturing, probably being the primordia of the apothecia.

Remarks

It seems impossible nowadays to get a clear idea of what *Peziza pinicola* really is. According to NYLANDER (cit. ETTLINGER), *Peziza pinicola* Rebent. (1804) is *Pseudographis pinicola* (Nyl.) Rehm.

FRIES, in his Syst. Myc. II. p. 113: 1823, described *Peziza pinicola* as follows "obovatus, extus fibrosa-striata, rugosa, fusconigricans, margine inflexo-fimbriata, disco expallente" and cited his exsiccatum no. 162. His description does not exclude the identity with *Crumenula pinicola* (Fr.) Karst.; but only a renewed study of the Fries's exsiccatum may solve this problem. KARSTEN, afterwards, has given a clear diagnose of *Crumenula pinicola* (exs. no 726 in Fungi Fennici). The citation of the latter author only, as was done by ETTLINGER is incorrect; FRIES must be cited between brackets.

BOUDRU (2) recorded damage due to this species to young corsican pine in Belgium. He succeeded in finding the apothecia on the infested branches. An imperfect form was never detected, which is confirmed by JØRGENSEN (13) and KUJALA (14).

In the Netherlands, VOORBEYTEL CANNENBURGH (21) recorded a serious injury of the stems of corsican pine, caused by a *Crumenula* species which he regarded as hitherto undescribed. No herbarium

specimen was left, but from his description of the fungus we have no doubt that he had found *Crumenula pinicola*.

It was supposed that this species has a saprophytical life. Sometimes, however, canker-like wounds were noticed on the stems and branches of *Pinus sylvestris* L. which were covered with numerous apothecia of this fungus. The same phenomenon was observed in corsican and austrian pine. In many cases wounds were seen to form a considerable amount of resin. Investigations on the pathology of this species were started, but up till now no proof of its parasitism could be given.

This Discomycete was collected from the following localities on *P. nigra* Arn. var. *austriaca* Asch. et Gr., *P. nigra* Arn. var. *corsicana* Schn. and on *P. sylvestris* L. The apothecia had not only developed on the bark of the stems, but in great numbers on the dead branches as well.

Specimens examined

Gelderland:

Ede, Ginkel, on *P. sylvestris*, 16-VI-1951, Gremmen 116
Loernermark, on *P. nigra* austr., 26-VI-1951, Gremmen 118
Loernermark, on *P. sylvestris*, 26-VI-1951, Gremmen 117
Nieuw-Soerel, on *P. nigra* cors., 16-IV-1942, v. Vloten 522
Vorden, Kieftenkamp, on *P. sylvestris*, 16-VII-1951, Gremmen 112
Wageningen, Oostereng, on *P. sylvestris*, 25-VI-1951, Gremmen 109

Utrecht:

Rhenen, Koerheuvel, on *P. sylvestris*, 16-VI-1951, Gremmen 96.

b. ***Crumenula sororia*** Karst., Myc. Fenn. I. p. 211: 1871.

Description (after 119)

Apothecia about 1–2.5 mm across. Stipe 300–600 μ . The excipulum consists of a compact tissue, yellow-green coloured and about 40–60 μ thick (textura intricata). The excipulum-wall has a dense tissue of

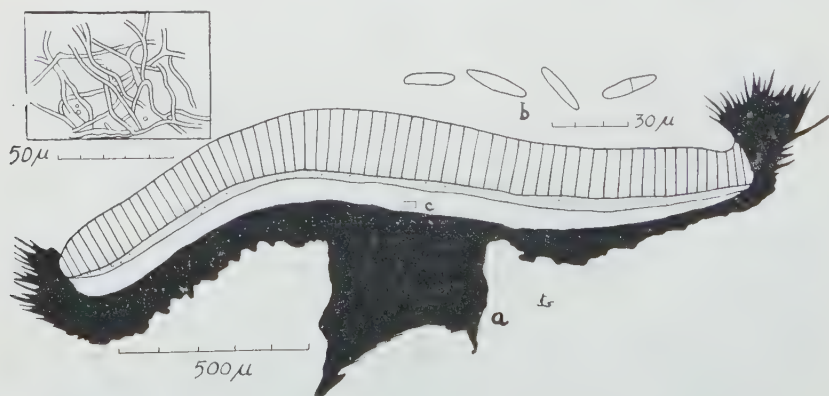


Fig. 3 *Crumenula sororia* Karst. a. apothecium (partly schematic); b. ascospores; c. part of the tissue of the excipulum

60–90 μ , becoming opaque externally and on the outside showing irregular cell-protuberances which towards the margo pass into hair-like projections up to 100 μ long. Hypothecium about 25–35 μ , yellow-green coloured. Hymenium about 130 μ thick, yellow-green. Epithecium wanting. Asci 86–114 \times 11 μ . Ascospores 12.9–30.1 \times 5.7 μ , colourless, 1-, 2-, 3- and 4-celled, ellipsoidal. Paraphyses filiform (Fig. 3).

Pycnidial Stage

This Discomycete species has a most characteristic imperfect stage which was often found and seems related to the genus *Sirothecium* Karst. (Symb. Myc. 20. p. 105).

The pycnidia are more or less globular, growing in groups or isolated on the substratum. They are black and measure 0.4 to 0.7 mm. The wall of the pycnidium is dark brown and consists of roundish, thick-walled cells with a diameter of 3.5 to 8.0 μ . A characteristic porus is lacking, the pycnidia open by rupturing of the cellwalls. On account of these features, this conidial stage may belong to the *Excipulaceae*.

The conidia (Fig. 4) are subhyaline or slightly green, mostly consisting of a system of many-celled branches. The main branch has 7 to 9 cells, mostly carrying 1 to 4 secondary branches, each of which consists of 1 to 5 cells. Sometimes a tertiary branch may be observed.

Each cell has rather thick walls and measures 5.5–5.7 \times 3.5–3.8 μ . The main branch varies from 30 to 50 μ in length and is terminated by an acuminate cell. The conidium which strongly resembles the fingers of a hand is as a whole shed from a subhyaline tissue which forms the inner wall of the pycnidium.

Since this stage of the Discomycete *Crumenula sororia* Karst. seems to be undescribed and, in fact, as we never found such characteristic pycnosporos in any of the existing genera of the *Excipulaceae*, the stage is considered to represent a new genus which the junior author proposes to name *Digitosporium*. The type species is *D. piniphilum* which was found on branches of *Pinus sylvestris* L. The type is deposited in the junior author's herbarium, the iso-type in the Leiden Herbarium.

Digitosporium piniphilum Gremmen gen. nov. spec. nov.

Ad familiam Excipulacearum pertinens. Corticola.

Pycnidia superficialia, atra, solitaria vel caespitosa, orbicularia vel oblongata, astomata, 0.4–0.7 mm in diam.

Corticis pycnidiorum cellulae, subglobosae, brunneo-atrae, 3.5–8.0 μ in diam.

Conidia magna, hyalina vel subhyalina, cellulis pluribus, digitiformibus interdum ramosa, 30–50 \times 3.5–3.8 μ .

Stadium perfectum: *Crumenula sororia* Karst. Myc. Fenn. I. p. 211: 1871.

Habitat: In cortice ramorum *Pini sylvestris*.

Typus: In Herbario J. Gremmen, 6-XII-1952, ex Herbario Fungi Fennici, leg. V. Kujala, sub *Crumenula sororia* Karst., pycnidia cum conidiis digitatis, N. Helsinki, Kulosaari, in *Pino sylvestre*, in ramis vivis, 14-IV-1944.

Other specimen examined (from the Netherlands)

Gelderland: Nunspeet, Willemsbosch, on *P. nigra* austr., 10-III-1949, Gremmen 631.

Culture results

Cultures were obtained from ascospores. The colour of the mycelium was greyish, while the growth resulted in the formation of globular colonies on cherry decoction agar. Isolates obtained from pycnospores were similar to those from ascospores. After 2½ months black pycnidia with typical pycnospores were developed. After aging these cultures also showed abundant greyish aerial mycelium, whilst a black pigmentation was diffused into the agar.

Remarks

REHM (18), primarily kept *Cr. sororia* Karst. and *Cr. pinicola* (Fr.) Karst. separated, but united them again in 1912.

GUYOT (11), in 1934, also assumed the existence of only one species, on the grounds that he had collected an intermediate form. There are, however, sufficient reasons to consider *Cr. pinicola* and *Cr. sororia* as good species, viz. the structure of the excipulum, the form of the ascospores and moreover the imperfect stage in *Crumenula sororia* Karst.

With regard to the pathology of *Cr. sororia* Karst., the senior author already in 1933 proved beyond doubt its parasitism, and found the characteristic imperfect stage at the same time.

FERDINANDSEN & JØRGENSEN (9) again reported on its parasitism, and also mentioned a pycnidial stage with dactyloid spores.

KUJALA (14) found this Discomycete to be very common in Finland, where it causes wounds and a formation of resin on the infested wounds. According to this author the conidial stage is much more common than the perfect form.

In the Netherlands, this Discomycete is always found on resinous cankers, occurring on stems and branches of *P. nigra* Arn. var. *austriaca* Asch. et Gr., on *P. nigra* Arn. var. *corsicana* Schn. and on *P. sylvestris* L.

Specimens examined

Gelderland:

Loenermark, on *P. sylvestris*, 6-III-1951, Gremmen 119

Nieuw-Soerel, on *P. nigra* cors., 16-IV-1942, v. Vloten 523

Nunspeet, on *P. nigra* austr., 10-III-1949, v. Vloten 111.

c. ***Scleroderris abietina*** (Lgbg.) Gremmen comb. nov.

syn. *Crumenula abietina* Lgbg., in Svenska Skogsvårdsfören. Tidskr. p. 9-44. 1913.

Description: (after 521)

Apothecia about 1 mm across. Stipe short, about 200 μ . The excipulum consists of polygonal, dark brown, thick-walled cells, 6-15 μ in diameter (textura prismatica). At the base this tissue is

70 μ , tapering towards the margo into the opaque excipulum-wall. On the outside the excipulum bears irregular cell-protuberances. At the margo there are scale-like projections, instead of hairs. Hypothecium 20 μ thick, colourless. Hymenium 60–70 μ thick, subhyaline.

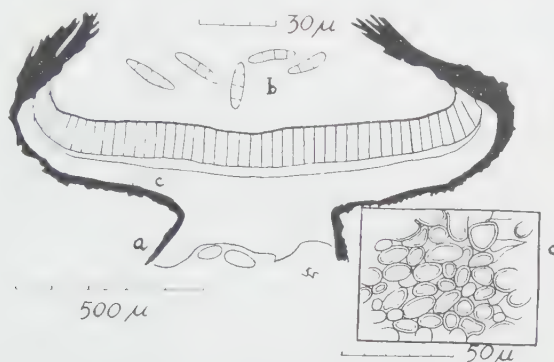


Fig. 5. *Scleroderma abietina* (Lgbg.) Gremmen. a. apothecium (partly schematic); b. ascospores; c. part of the tissue of the excipulum

Epithecium well-developed, 20–30 μ thick, brown. Asci 117.8–121.6 \times 11.4 μ . Ascospores 15.2–16.1 \times 3.8–4.7 μ , colourless, typically 4-celled, ellipsoidal. Paraphyses filiform (Fig. 5).

Pycnidial Stage

A pycnidial stage was always found in great numbers. This imperfect stage, *Brunchorstia pinea* (Karst.) v. Höhn. (confr. *Fragmente zur Mykologie*, p. 142: 1915) has dark brown pycnidia with falcate spores. These pycnosporos ooze out in delicate whitish to creamy tendrils and measure 26.0–47.7 μ . Out of 100 spores, 15 were 1-celled, 17 were 2-celled, 66 were 3-celled and 2 were 4-celled.

Culture results

In many cases *Cr. abietina* was isolated from the diseased twigs. Cultures obtained from ascospores produced characteristic pycnidia with pycnosporos. The mycelium was distinctly coloured and varied from green via yellow-green to greyish green.

Remarks

In 1926 a damage on corsican pine was reported in the Netherlands (Frederiksoord). Some years afterwards, in 1930, once again serious injury was observed in austrian and corsican pine ("de Delle" and Nieuw-Soerel). In 1944 a number of papers published by BOUDRU (3, 4, 5) appeared in Belgium dealing with this fungus. In one of these papers (5) the author mentioned 55 coniferous hosts of this Discomycete, most of which proved to be new. Curiously enough, he also described about 16 species of hardwoods (4) on which he found the fungus. In his opinion the species would be very common and certainly of saprophytical nature. These informations strongly suggest an error

on the part of the author, since hitherto *Crumenula abietina* is only known to occur in species of the genera *Picea* and *Pinus*. Fortunately, part of the material identified by BOUDRU was still available in the Forest Institute at Groenendael in Belgium for renewed study. Without exception the apothecia of the material on conifers proved to belong to *Pezizula livida* (B. et Br.) REHM, whereas those on hardwood were *Pezizula cinnamomea* (Fr.) Sacc. In none of these cases apothecia of *Crumenula abietina* Lgbg. could be detected, which was confirmed on re-examination of the material. We were almost certain that BOUDRU did not know *Cr. abietina*, which may account for the great number of new hosts recorded for this fungus. As far as we know, both *Pezizula*-species mentioned are saprophytes indeed.

ETTLINGER (8) studied a die-back of *Pinus*-species in Switzerland which was caused by *Cr. abietina* and KUJALA (14) described a serious attack by the same Discomycete on *Pinus Murrayana* Balf. in Finland.

In 1949 this fungus was again found in the Netherlands on *Pinus nigra* Arn. var. *austriaca* Asch. et Gr., where it occurred on the dying twigs. The trees showed the characteristic symptoms of the disease.

Specimen examined

Gelderland: Nunspeet, Willemsbosch, on *P. nigra* aust., 27-IV-1952, v. Vloten 521.

d. ***Scleroderis laricina*** (Ettl.) Gremmen comb. nov.
syn. *Crumenula laricina* Ettl., Diss. E. T. H., Zürich, 1945.

Description (After ETTLINGER, specimen collected on 18-VIII-1940)

Apothecia about 1 mm across. Stipe very short or lacking. The excipulum consists of a textura prismatica, 40–60 μ which is made up of more or less roundish, dark brown cells measuring 4–7 μ ; it passes into the opaque excipulum-wall which bears slight cell protuberances.

Hypothecium 22–38 μ thick, hyaline. Hymenium 60–80 μ thick, hyaline.

Epithecium wanting. Asci 63–118 \times 5–9 μ (cit. ETTLINGER). Ascospores 10–17 \times 3–4 μ , colourless, 2-celled, ellipsoidal (cit. ETTLINGER). Paraphyses filiform (cit. ETTLINGER). (Fig. 6)

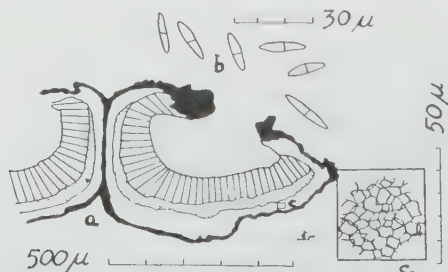


Fig. 6. *Scleroderis laricina* (Ettl.) Gremmen. a. apothecia (partly schematic); b. ascospores; c. part of the tissue of the excipulum

A characteristic imperfect form, *Brunchorstia laricina* Ettl. belongs to this fungus.

Culture results

Inoculation tests performed by ETTLINGER in Switzerland did not succeed. However, it was possible to isolate the fungus from fresh, diseased material.

Remarks

This species which was found in Switzerland (Kt. Graubünden and Kt. Bern) by ETTLINGER on branches of *Larix decidua* Mill. seems to be known from that country only.

Apothecia of this Discomycete were studied from the collections received from the "E.T.H." at Zürich.

c. ***Cenangium ferruginosum*** Fr. ex Fr., Syst. Myc. 2 (1). p. 187: 1822. syn. *Cenangium ferruginosum* Fr., Vet. Akad. Handl. p. 361: 1818.

Description (After 67)

Apothecia about 1–2 mm across, leathery. Stipe wanting. The excipulum consists of a loosely woven, hyaline tissue (textura intricata). At the base this tissue measures up to $400\ \mu$, gradually tapering towards the margo ($40\ \mu$). Excipulum-wall dark brown, consisting of roundish to angular cells, $20\text{--}100\ \mu$ thick. Further externally this wall is opaque and occasionally shows some cell protuberances on the outside. Hypothecium $35\text{--}75\ \mu$ thick, yellow-brown. Hymenium $75\text{--}100\ \mu$ thick, colourless. Epithecium wanting. Asci $80 \times 14\text{--}15\ \mu$. Ascospores $12\text{--}13 \times 5\text{--}6\ \mu$, colourless, 1-celled, ovate. Paraphyses filiform, somewhat clavate at the apex, septate. (Fig. 7)

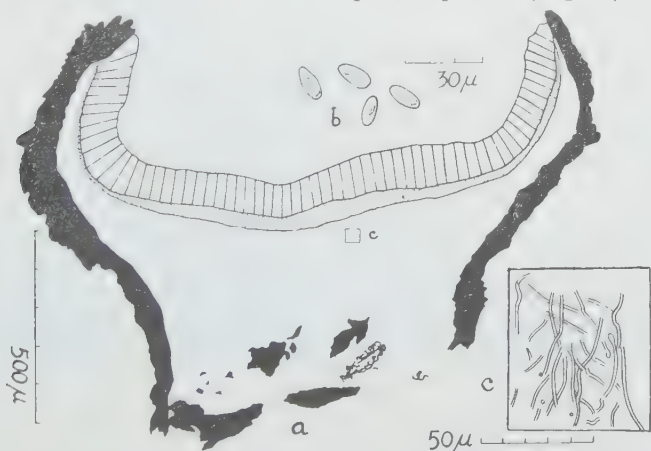


Fig. 7. *Cenangium ferruginosum* Fr. ex Fr. a. apothecium (partly schematic) b. ascospores; c. part of the tissue of the excipulum

Culture results

This fungus grew very slowly in vitro and had a green to yellowish green colour. After some time spermogonia with bacilliform spermatia

were formed, whereas under certain conditions it was possible to obtain mature apothecia in culture (GREMMEN, 1952).

Remarks

WEIR (22) successfully inoculated *P. ponderosa* Laws. with the ascospores of this fungus. It is possible that his spore suspension was contaminated with spores of *Brunchorstia pinea*, for this fungus was also observed on his trees in the field. It should be noted that at that time *B. pinea* was still considered the imperfect stage of *Cenangium ferruginosum*.

LIESE, in an oral communication, told the senior author that he always found the pycnidia of *B. pinea* on dying branches, whereas apothecia of *Cenangium* were never found. He, too, thought *Brunchorstia* to be the imperfect form of *Cenangium* and therefore only used the name of the perfect stage, which is common practise when this stage is known. LIESE considered the occurrence of *Cenangium* due to previous damage by some *Cecidomyia*.

BAXTER (1) reported a damage caused by this fungus on exotics. FERDINANDSEN & JØRGENSEN (9) doubted the parasitic nature of this fungus, showing that in most cases *Brunchorstia* was found on the branches. BOYCE (6), however, considered the fungus a parasite, but rarely ascribed damage to this Discomycete. Sometimes this fungus caused the so-called "pruning disease". KUJALA (14) regarded it a saprophyte with a slightly parasitic nature.

From our inoculation experiment, described below, it appeared that *C. ferruginosum* is a genuine saprophyte. Consequently, the die-back of *Pinus* in the above mentioned cases must be ascribed to *ScL. abietina*. (confr. Part III).

Usually this Discomycete is found on dead twigs of several species of the genus *Pinus*. The fructifications occur in small groups and when in dry condition resemble those of *Crumenula*.

Specimens examined

Gelderland:

Ede, Sliemer, on *P. sylvestris*, 28-IV-1947, Gremmen 23

Nunspeet, Willemsbosch, on *P. nigra* aust., 10-VIII-1948, v. Vloten 105

Otterloo, on *P. sylvestris*, 3-V-1951, Gremmen 4

Wageningen, Dorschkamp, on *P. montana*, 31-V-1948, Gremmen 67

Wageningen, Oostereng, on *P. sylvestris*, 25-VI-1951, Gremmen 5

f. Cenangium acicolum (Fuck.) Rehm, Krypt. Fl. p. 228: 1896.

Description (after 7)

Apothecia about 1–2 mm across. Stipe almost lacking. The excipulum consists of a hyaline textura intricata (a loosely interwoven tissue), at the base measuring up to 270 μ , at the margo about 40 μ thick. The excipulum-wall has dark brown roundish cells and is about 20–60 μ thick. Hypothecium about 40 μ thick, yellowish brown.



Fig. 8. Method of inoculation with pure culture; no. 2 has succeeded



Fig. 4. *Digitosporium piniphilum* Gremmen gen. nov. spec. nov.
Pycnospores and microconidia in a four months old culture

Hymenium about $80\ \mu$ thick, colourless. Epithecium wanting. Asci $70\text{--}96 \times 7.5\text{--}11\ \mu$. Ascospores $11.5\text{--}19 \times 4\text{--}4.5\ \mu$, colourless, 1-celled, sometimes 2-celled, acuminate, with 1 or 2 guttulae. Paraphyses with clavate apex.

Culture results

The growth of this fungus was very slow. On potato-dextrose agar the colour of the mycelium changed from white to cream, sometimes with greenish patches. After aging it turned via greyish blue to greyish white. Characteristic blackish brown ramifications were sometimes observed in the medium. On sterilized wheat-grains there was often a tendency of the mycelium to develop a yellowish colour. Neither spermogonia, nor imperfect stages were obtained in vitro, though this fungus was cultured for a long period.

Remarks

This species is a genuine saprophyte, occurring on dead needles of several species of *Pinus* and sometimes also on the twigs between the needles.

FUCKEL (Symb. Myc. p. 269: 1871–1875) considered this fungus a variety of *C. ferruginosum* Fr. ex Fr.

VON HÖHNEL (12) called this fungus *Encoelia acicolum*, but the whole structure of the apothecium shows a relationship with that of *C. ferruginosum*.

Specimens examined

Gelderland:

Nunspeet, Willemsbosch, on *P. nigra* austr., 28-VI-1948, Gremmen 7
Wageningen, Dorschkamp, on *P. sylvestris*, 19-X-1949, Gremmen 6

PART III

Investigations on the pathology of the fungi mentioned

The pathology of the species mentioned in Part II does not seem to have been studied in great detail. FERDINANDSEN & JØRGENSEN (p. 199: 1938) infected the tips of just opened shoots of *P. nigra* and *P. sylvestris* during June and July with conidia or mycelium of *Scleroderris abietina*. In the next year characteristic symptoms of the disease were observed.

THOMAS & TERRIER (cit. ETTLINGER) successfully executed bud and wound inoculations, from which they obtained the fungus *Scleroderris abietina* by means of re-isolation.

As regards *C. ferruginosum*, there is a short report by WEIR (22).

The senior author especially studied *Cr. sororia*, *Scl. abietina* and *C. ferruginosum* with regard to their pathology. For this investigation 21 trees from 6 to 7 years old were used, 7 of which were scots pine, 7 corsican pine and 7 austrian pine. Of each tree four equally developed

branches aged, 2, 3, 4 and 5 years were selected and wounded. The wounds were inoculated and labelled 1 to 4. In order to compare the results the four different inoculations were executed on one tree (fig.8). Before wounding, the part of the branch to be inoculated was cleaned with cotton-wool soaked in ethyl alcohol. Thereupon an incision was made with a flamed scalpel through the bark into the wood. The wounds were closed with sterile cotton-wool and paper of gutta-percha and the dressing tied with adhesive tape and raffia.

The execution of the inoculations was as follows:

1. With sterile cherry decoction agar.
2. With a pure culture of *Cr. sororia* on cherry decoction agar of about 4 months old, which had been isolated from 6–8 ascospores from apothecia occurring on *P. sylvestris*.
3. With a pure culture of *Scl. abietina* on cherry decoction agar of about 5 months old, which was isolated from one pycnospor of a pycnidium occurring on *P. nigra* var. *austriaca*.
4. With a pure culture of *C. ferruginosum* on cherry decoction agar of about 3 months old. This culture was isolated from one ascospore of an apothecium occurring on *P. sylvestris*.

The branches which had been inoculated in October were checked for results in December the following year.

TABLE I

Hostplant	Sterile agar	<i>Cr. sororia</i>	<i>Scl. abietina</i>	<i>C. ferruginosum</i>
<i>P. sylv.</i>	6 inoc. 0 inf.	6 inoc. 6 inf.	6 inoc. 0 inf.	7 inoc. 0 inf.
<i>P.n.aust.</i>	4 inoc. 0 inf.	7 inoc. 5 (+ 1) inf.	6 inoc. 0 inf.	6 inoc. 0 inf.
<i>P.n.cors.</i>	3 inoc. 0 inf.	7 inoc. 4 (+ 2) inf.	7 inoc. 3 (+ 2) inf.	6 inoc. 0 inf.

All wounds inoculated with sterile agar were negative. In some cases, however, a small resin flow was observed.

Inoculations executed with a pure culture of *Cr. sororia* showed a serious injury. In 56 to 100 percent of the wounds, small cankers had been formed, most of which showed pycnidia.

Inoculations with the fungus *Scl. abietina* only succeeded in *P. nigra* var. *corsicana*, where 42 to 70 percent of the trees were infected. In a number of these infections pycnidia were found on the dead needles.

Inoculations on *P. nigra* var. *austriaca* and on *P. sylvestris* always failed.

Wounds treated with a pure culture of *C. ferruginosum* always showed a negative result.

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LINNÉ's VIEWS ON THE HIERARCHY OF THE TAXONOMIC GROUPS

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It is the fate of most historic personalities that in the course of time their work sinks almost completely into oblivion, and that the few lingering reminiscences of their achievements are transmitted to later generations in the form of second- or third-hand quotations, usually mixed with more or less anecdotic episodes from their life. It must be admitted that LINNÉ occupies in this respect a comparatively favourable position, for most educated people will remember that they heard in their school days of at least three things which are credited to him, in the first place that he produced a classification of the plant kingdom which is based on the number of stamens and carpels, the so-called sexual system, in the second place that he was the first who consistently applied the binomial nomenclature, i.e. the custom to designate an organism by a combination of two names, viz. a generic and a specific one, and thirdly that he was the originator of the pronouncement "Species to numeramus quot diversae formae in principio sunt creatae" (We count so many species as in the beginning different forms were created). Other achievements of LINNÉ may have been of greater importance, but it is these three things for which he is most generally remembered.

The pronouncement quoted above, which means that the groups of individuals which form the species are descended from ancestors that owed their origin to an act of creation, derives its historic importance from the part it played in the debates on the theory of evolution. As it implies that the species are constant, it became the watchword of the antagonists. It is, however, rather strange that this pronouncement has so often been quoted, for it is found in LINNÉ's earlier works only, and was in the later ones replaced by another statement that flatly denies the constancy of the species.

The later pronouncement meant in the preceding paragraph is, like the first, found at different places in his work. It was first brought forward in the 1761 edition of his "Systema Plantarum", then in the dissertation "Fundamentum Fructificationis, prop. J. M. GRÄBERG, 1762" (reprinted in *Amoenitates Academicae* VI), and thirdly in the Supplement to the sixth edition of his "Genera Plantarum", which

dates from 1764. That I quote the doctor's thesis of his pupil GRÅBERG as a work of LINNÉ finds its justification in the circumstance that LINNÉ himself adopted the same attitude. He did this with regard to all the dissertations of his pupils, and when we see that his contemporaries too credited these works to him, it seems permitted to assume that they may indeed be regarded as his spiritual property. It can hardly be doubted that the redaction of these dissertations is by the hand of the promovendi; this appears from the striking differences in style and from the use of words that are not found in the works that LINNÉ edited under his own name. The explanation probably is that the subjects were first discussed at some length by LINNÉ, and that the latter asked the promovendi to write down the gist of the discussion. Howsoever this may be, it can not be denied that the dissertations published in the "*Amoenitates Academicæ*" are of the utmost importance for our knowledge of LINNÉ's views. LINNÉ's own works are written in the aphoristic style that was so much in vogue in the seventeenth and eighteenth century, and because of its exaggerated conciseness it is often difficult and not always possible to see what he really meant; in the dissertations, however, we find on the whole a methodical reasoning.

In the formulation used in "*Genera Plantarum*, ed. 6, 1764" the pronouncement which replaced the earlier one quoted in the introductory paragraph, runs as follows:

"1. CREATOR T. O. in primordio vestitit Vegetabile *Medullare* principiis constitutivis diversi *Corticalis*, unde tot difformia individua, quot *Ordines Naturales* prognata". (In the beginning the thrice exalted Creator covered the medullary substance of the plant with the principles of which the various kinds of cortex consist, and in this way as many individuals were formed as there are now Natural Orders)

"2. *Classicas* has (1) plantas Omnipotens miscuit inter se, unde tot *Genera* ordinum, quot inde plantæ". (The vegetable prototypes of paragraph 1 were mixed with each other by the Almighty, and there are now so many Genera in the Orders as in this way new plants were formed)

"3. *Genericas* has (2) miscuit Natura, unde tot *Species* congeneres, quot hodie existunt". (The generic prototypes of § 2 were mixed with each other by Nature, and in this way in every Genus so many Species were formed as at present exist)

"4. *Species* has (3) miscuit Casus, unde totidem, quot passim occurrunt *Varietates*". (The Species whose origin was explained in paragraph 3, were mixed with each other by Chance, and in this way the Varieties arose that here and there are met with).

The form in which these pronouncements are made, strikes us as strange and old-fashioned, and to some extent it was so already in LINNÉ's own time. We might perhaps be inclined to ascribe it to the influence of the atmosphere in which he grew up, that of the vicarage of Stenbrohult, but it seems more probable that it is, at least partly, due to the influence of that other remarkable Swede, the mystic SWEDENBORG. It is true that SWEDENBORG's name is nowhere mentioned

in the works of LINNÉ, but they must nevertheless have known each other rather intimately, for it is reported that SWEDENBORG was elected a member of the Swedish Academy on LINNÉ's recommendation. Although these two exceptional men were in many respects utterly different, there is an unmistakable similarity in the way in which they expressed their views. At any rate we must see LINNÉ against a background filled by men who were used to debate on theological questions and who even when the debate concerned questions of a different nature clothed their arguments in a theological form, and we should be careful not to place him in the circle of the physicists and physically orientated philosophers of that time: that was a world with which he had no contact, and for which he felt no interest. SACHS, the deserved plant physiologist of the preceding century, was in his "Geschichte der Botanik" certainly not always fair in his opinion of LINNÉ, could in fact not be fair to him because he was unable to cross the void that separated his own spiritual atmosphere from that of LINNÉ, but in one respect he certainly was right: LINNÉ was in most respects a man of the past; he was the dominating figure in an epoch of the history of plant taxonomy that was drawing towards its close. It is his great merit that he sifted the material that had been accumulated by his predecessors, and that he arranged it in an easily surveyable system, but the house that was built by him, although solid enough, was old-fashioned, and it was for this reason soon deserted; the foundations of the building in which plant taxonomy would find a more suitable home, were laid a quarter of a century after LINNÉ's death by ROBERT BROWN and AUGUSTE PYRAME DE CANDOLLE. These men expressed their views in a modern way, and were easily understood. That afterwards on the whole so little attention was paid to LINNÉ's ideas, even in those cases where they certainly would have deserved a better lot, is doubtless for a large part due to the antiquated form in which they were presented. The nineteenth century with its entirely different orientation was not interested in this kind of literature; in the biologists of that time it even will have awakened a feeling of aversion.

To this mental aversion it is probably due that LINNÉ's views on the nature and origin of orders, genera, species and varieties received no attention in the immediately following period. A quarter of a century later WILLDENOW, who was a very able and many-sided botanist and who, moreover, as the editor of a new and considerably enlarged edition of LINNÉ's "Species Plantarum" must have been well acquainted with the latter's works, makes no mention whatever of these views in his nevertheless fairly detailed handbook of botany. At a much later epoch, when the contention between the evolutionists and their antagonists had been decided in favour of the first, and it became a kind of sport to hunt for pre-Darwinists, these pronouncements of LINNÉ were once more unearthed in order to prove that LINNÉ too had been one of them. This, however, was doubtless a mistake. The theory of evolution assumes that all organisms, living and extinct, are descended either from a single prototype or else from a

small number of prototypes, but in LINNÉ's scheme first a rather considerable number, viz. fifty to sixty (v. infra) prototypes are created, and then out of the latter, which might be called the prototypes of the first order, by a manipulation of the Almighty himself fifty to sixty times as many prototypes of the second order are formed, i.e. 2500–3600, and as they are the vegetable prototypes only, this number has presumably to be doubled in order to account in LINNÉ's way for the diversity in the whole world of the living. This would mean therefore that LINNÉ must have assumed the existence of 5000–7200 prototypes, and this, I am afraid, is a number that no self-respecting evolutionist will swallow. We should, moreover, not overlook that LINNÉ's prototypes differ only in characters of minor importance from their descendants, and this too is hardly reconcilable with the intention of the theory of evolution. However, LINNÉ may nevertheless on account of this pronouncement be heralded as a precursor of modern views, for the picture it gives in the paragraphs 3 and 4 of the origin of species and varieties agrees in broad lines with the views developed in the first quarter of this century by LOTSÝ in his hybridization theory.

It is perhaps not superfluous to point out that nobody at present doubts the possibility that new species may arise as a result of hybridization; the only point on which there can be diversity of opinion, is, whether this is, as LOTSÝ assumed and as LINNÉ too had postulated, the only way in which they arise, or that there are more ways. However, we should realize that the origin of new species is a problem whose solution is but of subordinate importance to the theory of evolution. MACDOUGAL, the editor of DE VRIES' "Species and Varieties, their Origin by Mutation", printed on the fly-leaf of that work three statements, respectively from LAMARCK, DARWIN and DE VRIES, which illustrate the advance of our insight in the problem of the origin of species, but which reveal at the same time of how little avail this advance has been for the solution of the main problem of evolution, the origin of the more widely different groups. LAMARCK says "The origin of species is a natural phenomenon, DARWIN "The origin of species is an object of inquiry", and DE VRIES "The origin of species is an object of experimental investigation". DE VRIES expresses here the modern standpoint, but seen from this standpoint it is clear that there gapes a large gulf between this problem and that of the origin of the larger groups, where, as their representatives can not be crossed, experimental investigation is for the moment out of question.

I have said above that LINNÉ revealed himself in the paragraphs 3 and 4 of his pronouncement as a precursor of LOTSÝ's hybridization theory. To this end I had to assume, of course, that LINNÉ used the term "miscuit" (i.e. "mixed") in the sense of "crossed". Serious doubts as to the correctness of this interpretation are hardly admissible, for what other kind of mixing could he have observed in "nature" (paragraph 3), and what other kind of mixing could be "accidental" (paragraph 4)? In our time we might perhaps think of chimæras, but this kind of compound organisms were in the eighteenth century

unknown. The ample exposition of the theory in the dissertation "Fundamentum Fructificationis" moreover removes all our doubts, for here actual examples of hybridization are adduced in support. At first view it may nevertheless seem strange that LINNÉ should have thought here of ordinary crossing, for if two species are crossed, we are inclined to expect that the progeny will be more or less intermediary between the parents, not that the hybrids will all reveal themselves as varieties of the species to which the mother plant belonged.

LINNÉ's idea becomes comprehensible when we realize what he knew or thought he knew with regard to hybrids. That was very little indeed. It is true that hybrids are mentioned at various places in his works, but these so-called hybrids were, with a single exception, always aberrant specimens that were found either in the wild or in gardens, and for whose hybrid nature no sufficient grounds were adduced. How unfounded these assumptions sometimes were, is well illustrated by the fact that he once described a hybrid between a *Veronica* and a *Verbena*! Even the exception to which I referred above, a cross between two *Tragopogon* species, is not wholly beyond doubt. The only hybrids with which he was well acquainted, were those between the horse and the donkey, and as these hybrids always show a greater resemblance to the mother than to the father, he assumed that this was a general character of the hybrids, i.e. that they were all metroclinous. This is doubtless an error, although recent studies have shown that the phenomenon is not so exceptional as it was thought to be in the days that hybridization experiments were almost exclusively carried out with organisms that differed in varietal characters only. At any rate, in order to understand LINNÉ's scheme we will have to follow him in assuming that hybrids are always metroclinous. In the following paragraphs, in which his scheme is subjected to a detailed analysis, we will place ourselves on this standpoint.

In paragraph 1 of his pronouncement LINNÉ goes out from the supposition that the plant body consists of two main parts, the medulla and the cortex. The medulla is the essential part, for here finally the seeds are produced, and the latter are according to the traditional interpretation the main organs of reproduction. This essential part must be more or less the same in all plants, for it is because of this part that they and all their descendants are plants. The cortex, on the other hand, is, notwithstanding the fact that it produces the male organs, regarded as less essential. This too is part of the traditional interpretation, but it finds support in the supposed metroclinous character of the hybrids. Because of its less essential character the cortex is more variable in composition. In fact, LINNÉ assumes that there are fifty to sixty different kinds of cortex. This estimate is based on the number of orders that he recognized in his Natural System, for these orders were supposed to be derived from distinct prototypes. These fifty to sixty prototypes of the orders owed their origin to an act of creation. The medulla was to this end covered with a mantle of cortex that was composed of a mixture of different "principles", and of these mixtures fifty to sixty different ones must have been available.

What LINNÉ exactly meant with these "principles", is unknown to me. It may have been either the Aristotelean elements or the somewhat more numerous ones of BOYLE, but LINNÉ gives no further indication; in fact, it is even a riddle why he mentioned these "principles" at all. The point, at any rate, is that we have a medulla that we will indicate, because of its noble nature, with *A*, and round this medulla a mantle of cortex, which may be of various composition, and which, as it consists of more common clay, we will indicate with a small letter. The fifty to sixty prototypes of the orders therefore may be designated with the letter combinations *Aa*, *Ab*, *Ac*, etc. For simplicity's sake we will confine ourselves to the orders *Aa*, *Ab* and *Ap*.

In paragraph 2 of LINNÉ's pronouncement these prototypes of the orders are mixed with each other. This means that the egg cells¹ of the prototype *Aa* are fertilized with male cells derived from the other prototypes, and so on. Under normal circumstances a cross between representatives of different orders is impossible, and for this reason LINNÉ invokes here the aid of the Almighty.

The egg cells are supposed to be derived from the medulla, an erroneous view that was founded on LINNÉ's interpretation of the flower, or, to be more precise, on one of his interpretations of the flower, for in his works two interpretations are found side by side. According to the first, which LINNÉ based on views that via CESALPINO were borrowed from ARISTOTLE and THEOPHRASTUS, the calyx is derived from the "outer" cortex, the corolla from the phloem, the stamens from the xylem and the carpels from the medulla, whereas according to the second interpretation sepals, petals, stamens and carpels are homologous parts, which evidently would be impossible if they really were derived from different layers of the growing point. The incompatibility of these two interpretations apparently escaped LINNÉ's attention, but this is a point that falls outside the scope of this paper. It is sufficient to realize that at this occasion LINNÉ based his conclusion on the first interpretation, according to which the carpels, and therefore the egg cells too, are derived from the medulla.

The male cells are produced by the stamens, and the latter, as stated above, are supposed to be derived from the xylem, which is a part of the cortex mantle by which the medulla was surrounded. They may therefore be indicated as *a*, *b*, and *p*. Now, however, we are confronted with a difficulty, for if the egg cells of all the prototypes created in paragraph 1 were *A*, the combinations would produce no new forms. In order to save the situation LINNÉ therefore must have introduced an auxiliary hypothesis. He must have assumed that the medulla of these fifty to sixty prototypes before going over to the production of egg cells must have undergone a change, which, of course, would have been due to influences exercised by the fifty to sixty different kinds of cortex. In this way the medulla of the prototype *Aa* would have been changed into *A_a*, that of the prototype *Ab* into

¹ The terms "egg cells" and "male cells" are used here and in the following paragraphs for the sake of convenience. LINNÉ himself spoke of "ovules" and "pollen".

A_b , that of Ap into A_p . LINNÉ does not mention this auxiliary hypothesis, but in the aphoristic writings of that time such omissions are not uncommon. Moreover he will not have felt the need for it, for as the fruits are in the various orders of a different kind, he will have found it self-evident that their medulla too must have been, to some extent, different, and these differences could have had no other cause than the different composition of the cortex.

The egg cell A_a of the prototype Aa gives with the male cells a , b and p the combinations A_aa , A_ab and A_ap , the egg cell A_b of the prototype Ab gives with the same male cells the combinations A_ba , A_bb and A_bp , whereas the egg cells A_p of the prototype Ap gives with these male cells the combinations A_pa , A_pb and A_pp . Therefore, in the order Aa in this way the prototypes of the genera A_aa , A_ab and A_ap are formed, in the order Ab the prototypes of the genera A_ba , A_bb and A_bp , in the order Ap the prototypes of the genera A_pa , A_pb and A_pp , i.e. in each of the fifty to sixty orders in this way fifty to sixty genera are produced, altogether therefore 50^2 to 60^2 , i.e. 2500–3600. When this result had been reached, the direct influence of the Almighty was no longer required, and the origin of the species and varieties is in the paragraphs 3 and 4 of LINNÉ's pronouncement left to nature and chance. The mixing of prototypes of genera belonging to different orders therefore is excluded, for this does not happen under natural circumstances. However, even if it had been possible, it would not have led to the origin of a greater number of new forms, for the cortex consists, as we have seen, in all orders of the same fifty to sixty different kinds.

In the different genera too the medulla will undergo an influence of the cortex. In the genus A_aa it will become in this way A_{aa} , in the genus A_ab it will be changed in A_{ab} , in A_ap in A_{ap} ; in the genus A_ba it will become A_{ba} , in the genus A_bb in A_{bb} , in A_bp in A_{bp} ; in the genus A_pa it will be changed in A_{pa} , in A_pb in A_{pb} and in A_pp in A_{pp} . It are therefore egg cells of this constitution that combine with the male cells a , b and p . In this way we obtain in the genus A_aa the species A_{aaa} , A_{aab} and A_{aap} ; in the genus A_ab the species A_{aba} , A_{abb} and A_{abp} ; in the genus A_ap the species A_{apa} , A_{apb} and A_{app} ; in the genus A_ba the species A_{baa} , A_{bab} and A_{bap} ; in the genus A_pa the species A_{paa} , A_{pab} and A_{pap} , etc. As in each genus therefore fifty to sixty species are formed, the total number of species will lie between 50^3 and 60^3 , i.e. between 125000 and 216000.

In the same way we might obtain in each of these 125000 to 216000 species fifty to sixty varieties, but this is not to be expected, for accidents, of course, can not be expected to happen so regularly as what is decided by the clockwork of nature, which is set in action by the Almighty himself.

As it may after all seem somewhat strange that LINNÉ postulated but one kind of medulla, whereas he saw no objection against the assumption of fifty to sixty different kinds of cortex, it is perhaps not superfluous to enter somewhat deeper into this problem than we have done above. At first view it might look simpler to assume the existence of fifty to

sixty different kinds of medulla in order to explain the differences in the constitution of the egg cells of the fifty to sixty prototypes of the orders. However, there are two reasons for LINNÉ's choice. The first reason has already been mentioned; it is found in the important place assigned by LINNÉ to the medulla in the life of the plant. To us the medulla is a comparatively unimportant part, which often disappears at an early stage, but to LINNÉ it was what it had been to ARISTOTLE and CESALPINO, viz. the part that harboured the vegetable principle of life. The latter is, of course, the same in all plants, and it was therefore reasonable to suppose that the part by which it is carried was, at least in the beginning, also everywhere the same. The main reason for the assumption that the medulla must be regarded as the seat of the vegetable principle of life, is apparently found in its central position; the central part is evidently the noblest one. That LINNÉ was accessible to this kind of, in our eyes futile, speculations, can not be doubted. However, the second reason will probably have carried more weight with him. If we assume that there are already in the beginning fifty to sixty different kinds of medulla, the origin of the 2500—3600 different genera by the exchange of the fifty to sixty different kinds of cortex is, of course, easily understandable, but in order to explain the origin of the 125000—216000 species, we would have to assume that the medulla in the prototypes of the genera undergoes a change, and this change could, of course, only be due to an influence exercised by the cortex, and if the latter exercised such an influence in the prototypes of the genera, there is no reason to assume that it could not have exercised a similar influence in the prototypes of the orders. This means that LINNÉ's supposition of an originally uniform medulla is indeed preferable.

In the preceding paragraphs I have tried to demonstrate that LINNÉ's theory, if we accept his premise that the egg cells are derived from the medulla and the male cells from the cortex, is indeed acceptable. However, his other suppositions too require a critical consideration.

The main difficulty lies in the contrast between the first two paragraphs of his pronouncement and the third and fourth ones. In the first two paragraphs the result is achieved by the action of a supernatural power, in the two subsequent ones it is due to crosses that are carried out by nature or that are left to chance. In the first paragraph we are faced by an act of creation, and in the second with a process that although of a similar nature as the crosses meant in the next two paragraphs requires the intervention of the Allmighty. The crosses between genera belonging to the same natural order are in paragraph 3 left to nature. LINNÉ apparently was of opinion that these crosses offered no difficulty, which shows once more how small the knowledge of the phenomena of heredity in LINNÉ's time still was. Intergeneric hybrids are in reality very rare, and where they are met with, the difference between the genera is often so small that it might be better to unite the genera. The intergeneric hybrids mentioned by LINNÉ himself are, moreover, without exception products of faulty observation

and uncritical inference. In contradistinction to these intergeneric crosses the interspecific ones of paragraph 4 are supposed to be accidental. However, what LINNÉ really meant with the terms "natura" and "casus" is not clear, but that there must have been in his opinion a fundamental difference between the two, need not be doubted. I suppose that he assumed that the intergeneric crosses were carried out according to an immutable plan, and that "nature" therefore must be seen here as a kind of demiurge who executes God's intentions. In that case the difference between the crosses meant in paragraph 2 and the intergeneric ones of paragraph 3 would be that the first were carried out immediately after the prototypes of the orders had been created, whereas the latter are still in progress. This would explain why not all genera exhibit the total number of possible species (50-60). The comparative rarity of the varieties and their irregular occurrence will probably have induced LINNÉ to regard them as "accidental".

If we wish to criticize the theory, we may point out that it is applicable to plants only. It is true that in one of the medical dissertations reprinted in the "*Amoenitates Academicæ*" a similar scheme is developed for the animal kingdom. The central nervous system is here regarded as the seat of the principle of life, and the ovaries are directly derived from the latter, but as the remaining tissues are also derived from the central organ, be it in a more indirect way, this scheme is not directly comparable with the one we are discussing here.

If we confine ourselves to the kingdom of plants, we may state that by no means all plants are provided with medulla and cortex, which means that the theory is applicable to a part of the plant kingdom only. The fact that not all hybrids are metroclinous means that it is built on an unfounded generalisation, and the circumstance that in the paragraphs 1 and 2, where natural means are insufficient to produce the desired effect, the aid of a super-natural power is invoked moreover, places the theory outside the domain of natural science.

This seems to be a crushing verdict, and the reader may wonder why I did not place these critical remarks in front. It looks at first view as if the whole further discussion might in that case have been suppressed. However, when we consider the matter at somewhat closer range, we will realize that our critical remarks merely concern LINNÉ's explanation, not the factual contents of his pronouncement. The explanation probably was to him, as I will try to expound hereafter, but a matter of secondary importance. What he really wanted to say, is that there are in his opinion among the taxonomic groups of the plant kingdom four different ranks, viz. the natural order, the genus, the species and the variety, and that the differences between these ranks are of fundamental importance. The latter is expressed in a parabolic way by referring the origin of the orders to an act of creation, that of the genera to a direct intervention of God, that of the species to the regulating activity of nature, and that of the varieties to indeterminate influences. LINNÉ's earlier pronouncement, according to which the species owed their origin to an act of creation, is to be understood in the same way. In reality LINNÉ was not

interested in the creation, but what he wished to express in this rather unusual way is that the species are constant, an opinion which he modified to some extent, as we have seen, in later years.

The idea that the differences between the taxonomic groups of various ranks are of fundamental importance, must have been born in his mind when he occupied himself with the elaboration of his natural system. A natural order or, as we now say, a family like the *Umbelliferae* is more sharply defined than the genera of which it consists, and the various genera are more easily distinguishable than the species. The idea therefore rests on experience. However, that was in those days not considered sufficient; the observed facts required an explanation, and in the production of such explanations LINNÉ never was at a loss. In order to show of what kind these explanations were, I will cite here an example derived from another field of his activity. The explanation I have in mind, is at first sight perhaps not so strange as the set of suppositions by which he tried to make the hierarchy of the taxonomic groups acceptable, but if we enter somewhat deeper into the question, it will prove to be at least as unsatisfactory. It relates to his sexual system.

LINNÉ was at first fully convinced that his sexual system was a natural one. It had to be regarded as such because it was based on parts that are of primary importance for the survival of the plants, viz. the stamens and the carpels; by varying the number, the relative size and the degree of mutual dependance of these fundamental parts God had produced the various groups that were recognized by LINNÉ. This explanation apparently pays no attention to the fact that stamens and carpels are not the only parts of the plant that are of importance for its survival, i.e. that there are other parts on which the classification might have been based with as good right. In fact, some of his predecessors, who stood on the same standpoint, had based their classifications on the fruit and the seed, and theoretically it ought to have been possible to base it on the root, as the latter according to the then accepted view was the only organ that serves for the intake of food, which, of course, is a function as important as reproduction. It is almost unthinkable that LINNÉ would have overlooked these objections, and one gets the impression that he merely added the explanation because he did not want to break with an old custom. He may have reflected that without such an explanation his system might have been unacceptable to his contemporaries, and in this he was probably not far wrong. There is, in my opinion, good reason to regard LINNÉ's entirely superfluous and largely meaningless explanation of his sexual system as a concession to the spirit of the time, and if this view is accepted here, there is every reason to accept it in all similar cases. With regard to the explanation that LINNÉ supplemented to his views on the hierarchy of the taxonomic groups, it is, however, fair to admit that it is from a purely formalistic standpoint a marvellous achievement. With regard to his explanation of the sexual system this can certainly not be said.

The problem for which LINNÉ in his pronouncement on the

taxonomic groups of different rank had offered a solution, may be formulated as follows: are the differences between the groups of different rank of fundamental importance or should we assume that one rank gradually merges into another. We may put the question also in this form: is it possible to decide whether a group of individuals which show a certain degree of similarity, form a variety, a species, a genus or a natural order (I use here LINNÉ's terminology; at present we recognize a much larger number of ranks, but this is here of no importance). These are the questions for which LINNÉ had sought an answer, and the conclusion at which he had arrived, was that the differences between the various ranks were of a qualitative nature. This conclusion is in itself not so very important, for it is for a good deal intuitive, but it proves that LINNÉ had recognized the presence of this problem, and that certainly is worth noting.

Even now the problem formulated in the preceding paragraph is often overlooked. This finds its explanation in the circumstance that most biologists have not been able to free themselves from the ideas of the orthodox evolutionism. To the earlier evolutionists this problem indeed did not exist. LAMARCK as well as DARWIN assumed a nearly unlimited fluctuating variability, and this, of course, excludes the possibility that differences of fundamental importance might be present between the various organisms or groups of organisms. The differences they observed in nature, were to them of an accidental character only, for they owed their origin to the disappearance of groups of variates, the notorious "missing links". Subsequent investigations, which were based on DE VRIES' theory of the gene, have demonstrated the untenableness of this view. The splitting observed in the progeny of hybrids has taught us that the differences are by no means gradual, but that they are sharply defined, and rest on the presence or absence of definite genes. The discontinuity between the various groups of organisms can therefore no longer be doubted, but it remains an open question whether the differences between the groups of higher rank are of the same kind as those between the varieties, though, of course, more numerous, or that they are partly of an entirely different nature. This is a problem on which the study of the phenomena of heredity so far can throw no light, and for the present it is left therefore to the taxonomists to look for a solution. Most of the latter will doubtless be inclined to regard the various taxonomic ranks as qualitatively different, because this seems to be a sound base for the construction of a natural system, but they are just as LINNÉ unable to prove the correctness of this view. It is the standpoint of CUVIER in his controversy with ST. HILAIRE, which GOETHE in his old age witnessed and in which he displayed such a lively interest; the controversy is still actual, but it is now confined to the groups of higher rank.

The genes that are responsible for differences of a varietal character apparently return in widely different groups, and in this respect they remind us of the constituents of the various kinds of cortex postulated by LINNÉ. We have seen that the latter assumed that the different

kinds of cortex returned in different groups. The characters of the groups of higher rank, e.g. the presence of a pollen tube in the *Phanerogamae*, and the particular structure of the gynaeceum and of the ovule in the *Angiospermae*, are on the other hand confined to single groups, and can therefore hardly be ascribed to the presence of exchangeable genes. It seems reasonable to assume that they rest either on non-exchangeable genes or else on hereditary structures of an entirely different kind. LINNÉ might have given them a place in the medulla.

LINNÉ recognized the existence of a hierarchy among the taxonomic groups and he saw that this presented a problem. He also offered a solution of this problem, viz. that the differences between the various ranks are of a fundamental nature, but he was unable to advance arguments for this view. Such arguments are at the present moment too almost entirely wanting. That the taxonomists are on the whole inclined to accept the presence of fundamental differences between the various taxonomic ranks, rests on their conviction that without this assumption the construction of a natural system would lose a good deal of its significance.

